AN ELEMENTARY MANUAL
of
PHYSIOLOGY

FOR COLLEGES, SCHOOLS OF NURSING, OF PHYSICAL EDUCATION, AND OF THE PRACTICAL ARTS

BY

RUSSELL BURTON-OPITZ

S.M., M.D., PH.D.

Associate Professor of Physiology, Columbia University, and
Professorial Lecturer in Physiology in Teachers'
College of Columbia University

ILLUSTRATED

PHILADELPHIA AND LONDON

W. B. SAUNDERS COMPANY

1922

MADE IN U. S. A.

PRESS OF
W. B. SAUNDERS COMPANY
PHILADELPHIA

PREFACE

The teachers of physiology in our Medical Schools are greatly handicapped at the present time by the fact that the material which must necessarily be presented to the students in preparation for their clinical years, is so complex that it can scarcely be dealt with in detail in the number of hours of teaching ordinarily allotted to this science. It would indeed be very helpful if the matriculates in medicine could also present certain credits in elementary physiology, in addition to those obtained in biology, physics and chemistry. The only objection that might be raised against the establishment of more extensive courses in elementary physiology in colleges is that this change would tend to cause these institutions to lose their identity and purpose even more than they have at the present time. Obviously, a college is intended to disseminate general knowledge and not knowledge of a special or professional type. Thus, a college which permits its matriculates to crowd diverse courses in the fundamental sciences into the first two years of its curriculum and then passes these young men and women on to the medical schools, fails utterly in its purpose as a means of acquiring general culture.

It is evident, however, that the mission of physiology is much greater than that of serving as an essential link in the chain of medical subjects, because it also possesses an eminently practical value as a general study. This fact is recognized more and more from year to year. Thus, many States now require elementary courses in physiology in preparation for licenture in teaching in secondary schools and high schools. These raised requirements have greatly aided in destroying the erroneous conception of the schoolboy that physiology is essentially a discourse upon the evil consequences of smoking tobacco and drinking alcoholic beverages. Since physiology seems to have been presented

chiefly from this viewpoint, it cannot surprise us to find that this subject has always been distinctly unpopular with the pupils of the secondary schools. As stated above, the better training of these teachers will soon change this attitude of the pupils, because physiology, if properly presented, cannot fail to arouse their undivided interest.

Physiology is destined to fulfill an even more important mission in institutions for the training of nurses and dietitians. To this group of young men and women are to be added the constantly increasing numbers of students of physical education. Clearly, all these men and women should be thoroughly familiar with the structure and functions of the human body as compiled from data pertaining to living matter in general. It is obvious, however, that the material which may justly be presented to them, must be more elementary in its character than that offered to the students of medicine.

In order to meet the demands at this University, I established some years ago certain courses in elementary physiology which are now attended by more than three hundred students during each academic year. These courses consist of one to two hours of lecture and two hours of practical work each week, or of about one hundred to one hundred and twenty hours in all. The publication of this book has been stimulated by my desire to supply these students with a text presenting the subject-matter of physiology in as simple and logical a manner as possible. If I have succeeded in this, I hope that these pages will also be favorably received elsewhere, and aid materially in the dissemination of physiological knowledge among those men and women who are not directly concerned with medicine but are nevertheless entitled to the benefits that are surely to be derived from this study.

R. Burton-Opitz.

Columbia University,
New York City,
February, 1922.

CONTENTS

PART I

THE PHYSIOLOGY OF MUSCLE AND NERVE

SECTION I

GENERAL PHYSIOLOGY

CHAPTER XIX

CHAPTER XX

PART IV

NUTRITION

CHAPTER XXI

CHAPTER XXII

CHAPTER XXIII

CHAPTER XXIV

CHAPTER XXV

CHAPTER XXVI

CHAPTER XXVII

CHAPTER XXVIII

CHAPTER XXIX

PART V

THE NERVOUS SYSTEM

CHAPTER XXX

CHAPTER XXXI

PART I

THE PHYSIOLOGY OF MUSCLE AND NERVE

SECTION I

GENERAL PHYSIOLOGY

CHAPTER I

LIVING MATTER

Definition and Scope of Physiology.—Science is accurate knowledge acquired by means of exact observation and correct thinking. This definition suggests that scientific knowledge is gained by an analytical study of matter as it exists in nature. The universe is composed of different materials, such as earth, air, and water, which are collectively designated as matter. But, this enunciation does not betray to us what matter actually is, because our knowledge regarding its origin and basic structure is as yet very incomplete. It is permissible, however, to speak of certain definite forms of matter as bodies, and of matter of a rather conscript character as substances.

Science deals with the structure and behavior of matter in accordance with well established physical and chemical laws. This method of investigation creates a sharp dividing line between true scientific knowledge and that of a more or less speculative kind. Accordingly, the person who pursues this means of discovering and analyzing hitherto unknown facts pertaining to matter may be termed a scientist. It is obvious, however, that scientific knowledge may also be

acquired from the writings of persons who have been actively engaged in this kind of work. No difference can be noted between a student of this character and one seeking to obtain a knowledge of Latin or Greek. Their methods of study are practically identical, although the quality of their knowledge differs. Admittedly, however, such a student cannot justly be called a scientist in spite of the fact that the acquisition of scientific data requires a practical trend of mind which will enable him to analyze the condition and behavior of matter in an introspective manner. Like the carpenter or plumber, the true scientist derives his knowledge in a practical way in the workshop, and does not rely solely on books and didactic expositions for his information.

Although it is commonly held that all matter is dynamic, it may be stated at this time that it presents itself to the layman essentially in two forms: namely, as living or organic and as non-living or inorganic matter. The inanimate material is dealt with by the sciences of physics and chemistry, and the animate, by the science of biology. Accordingly, biology may be defined as the science which treats of matter when it is in the living state. Strictly speaking, however, matter does not retain a perfectly static condition for any length of time. Even the stones may be said to live, because their formation was attended with definite creative processes, while their apparently static existence is largely one of constant deterioration. In fact, some even acquire material and may, therefore, be said to be growing. It is true, however, that their creation and growth present certain details which are not directly discernible in the life of an animal. A mass of gun powder may be made to burn and explode. Likewise, it is a biological truism that an animal is capable of reducing certain substances from which it then derives a sufficient amount of energy to manifest life. It cannot be accepted as a fact that these phenomena of the inorganic and organic worlds are wholly different in their nature, because the principle involved in these processes is obviously the same, although it presents a somewhat different aspect in accordance with the kind of matter undergoing the decomposition.

While this question may be debated at some length, the beginning student should remember that the biological sciences deal with the phenomena presented by living matter, while the abiological sciences treat of those manifested by non-living matter. Accordingly, biology may be divided first of all into two sub-sciences: namely, zoölogy and botany. The former concerns itself with the gross appearance of animals, and the latter, with that of plants. The processes of life, however, are the same in both forms, and only when studied in a superficial manner can we recognize definite differences between them.

We may approach the study of living matter from two standpoints, taking cognizance either of the structure of its different components, or of their individual or joint action. The maker of a clock first of all familiarizes himself with the character and number of the wheels and cogs which go to form the entire mechanism before he actually joins them in an attempt to discover how they fit into one another and move. Quite similarly, the study of the heart or eye is scarcely feasible without first having obtained a clear idea regarding the general arrangment and structural details of these organs. Accordingly, we may represent the scope of biology as follows:

- Living Matter
  - Origin, development, and classification: (embryology, zoölogy, and botany)
  - Structure
    - General Morphology
      - Animals
      - Plants
    - Special
      - Gross (anatomy)
      - Minute (histology)
  - Function
    - General Physiology
    - Special Physiology

Physiology is the study of the dynamics of life. Its purpose is to analyze the processes occurring in living matter. It is true, however, that a study of the phenomena of life cannot well be attempted without a knowledge of the abiological sciences, because in many instances physiology consists merely of a study of the physics and chemistry of living

material. It need not surprise us, therefore, to find that the progress of physiology is closely interlinked with the development of the aforesaid sciences, because every new physical and chemical fact must greatly aid us in throwing additional light upon the behavior of living matter. Since the structural sciences, such as anatomy and histology, occupy a much more independent position in this regard, it has been possible to advance them at a much faster rate than physiology. For this reason, anatomy was able at an early date to assume a controlling influence in medical education, its preponderating position having been seriously contested by physiology only in more recent years.

Physiology belongs essentially to the nineteenth century and is, therefore, a comparatively new science. In spite of its youth, however, it presents a wealth of very valuable and highly interesting information which finds its most direct application in medicine, an art purposing the relief of suffering and prolongation of life. Its decidedly practical character, however, has also gained for it an unfaltering place in general education. Admittedly, everybody ought to attempt to gain a rather concise idea regarding the functions of the different organs of his body, so that he may be in a more favorable position to take care of what has been entrusted to him by Nature. In the form of general knowledge, physiology will aid us very materially in mastering and eradicating those forces of nature which tend to enfeeble us. Hence, its goal is the welfare of mankind.

Protoplasm.—The term protoplasm is derived from the Greek words "first form," and is applied in a general way to all types of living matter. In the words of Huxley, it constitutes the physical basis of life. This material presents itself as a rule as a semi-fluid, viscous entity, possessing a reticulated appearance, very similar to that of a cluster of soap-bubbles. Hence, however simple its organization may be, it always consists of a relatively resistant framework and a homogeneous watery ground substance.

When living matter is subjected to chemical analysis, its constitution immediately undergoes certain very fundamental changes which soon make it impossible for it to

manifest its ordinary processes of life. But in spite of the destruction of its function, such an analysis invariably proves that it is not composed of a single substance, but of several, which are combined in such a way that they may interact with one another producing a chemical basis for life. Living matter is somewhat like a proteid, because it always contains the element nitrogen. In addition, it embraces carbon, hydrogen, oxygen, sulphur, and phosphorus. Chiefly by admixture, it may also acquire calcium, sodium, potassium, silica, and other elements. Accordingly, protoplasm or living matter is made up of six primary constituents to which others may be added until it embraces sixteen of the elements now known to chemists. We do not know precisely how these constituents are arranged to give rise to protoplasm and hence, it is quite impossible at the present time to form it artificially in a test tube. And even if we should succeed some future day in producing it, we would still be confronted by the problem of causing it to undergo those peculiar changes which enable it to evolve its characteristic life processes.

The Origin and Evolution of Protoplasm.—While most astounding discoveries have been made in recent years, it is very doubtful whether the origin and character of the universe will ever become fully known to us. In the abiological as well as biological sciences the number of known facts is really insignificant in comparison with the totality of still unknown facts. It is questionable whether this relationship will ever be reversed. The scientist is an optimist in this regard, as may be gathered from his attempt to explain the formation of the now perfectly conscript bodies of the solar system by the nebular hypothesis. Likewise, the biologist has endeavored to elucidate the origin of life upon this planet by stating that protoplasm originated at a time when the cooling of the earth favored the molecular union between several of its most essential constituents. One globule of living substance so formed then gave rise to two, and these in turn to more complex entities. This direct descent of the species has been more fully established by Darwin, but naturally, the facts presented by this scientist deal only with the

production of definite modifications and new types and cannot justly be applied to the origin of protoplasm.

The earth is inhabited by a most perplexing variety of protoplasmic entities. Some of these appear as extremely small particles of living matter, pursuing a free and independent existence, while others are composed of several particles bound together to lead a communal life of the simplest type. When ascending the scale of the Animal Kingdom from the protozoa to the amphibia, reptilia, fish, birds and mammals, we eventually arrive at comparatively large masses of living matter which owe their existence chiefly to the fact that their protoplasm is divided into a multitude of small globules, each of which is rendered more compact and stable by a firm investing membrane. In the absence of this organization, the larger aggregates of protoplasm would soon split into much finer particles; in fact, even the smaller ones would not hold together without a certain compactness of their surface layers. It is essential, therefore, that protoplasm assume a definite structural unity, and unity of structure invites unity of purpose or function. A particle of protoplasm of this kind constitutes a cell. Accordingly, it must be evident that the term protoplasm is a very general one, being synonymous with living matter, whereas the term cell refers to conscript entities of protoplasm capable of independent function.

In the higher forms, many of these globules of organized protoplasm are united with others into larger masses or tissues. Hence, a tissue may be defined as a collection of cells possessing similar characteristics. Again, several tissues may be combined to form an organ. Accordingly, an organ may be said to be an aggregate of several tissues fulfilling a common purpose, but this definition should not convey the impression that the functions of its components are absolutely identical, because every organ consists first of all of a framework or web, the purpose of which is to give lodgment to its real functional element. In the case of the kidney, for example, it should be noted that its most important structural unit is the urinary tubule, while its capsule and internal septa of connective tissue merely lend compact-

ness to the entire structure. In addition, every organ contains a certain amount of nervous tissue which controls its function, and also numerous nutritive supply channels in the form of bloodvessels and lymphatics.

It is usually stated that bone, muscle, and blood are tissues, although it is apparent that a muscle, such as the biceps, is really made up of several tissues and should, therefore, be designated as an organ. It embraces a certain amount of connective tissue in which a large number of muscle cells are embedded, and in addition also nervous tissue, bloodvessels, and lymphatics. Quite similarly, it may not be evident at first sight that blood is a tissue, because it is made up of many independent cellular elements which are suspended in a fluid intercellular substance, known as the plasma. Blood is as truly a tissue as bone, the only difference discernible between them being that the latter remains stationary, whereas the former is moved from place to place.

When several organs are joined to form a single entity, we obtain what is known as an organism. Consequently, an organism may be defined as a colony of organs, each of which unfolds its own peculiar function in order to maintain the welfare of the whole. In the highest forms, these organs are arranged in groups, giving rise to systems, such as the circulatory, respiratory, nervous, digestive, excretory, and generative; but while each system embraces a number of different organs, its functional product is uniform in character. This fact is well illustrated by the circulatory system which embodies a pumping station or heart, and a large number of membranous channels by means of which the nutritive fluids are distributed to all parts of the body. Likewise, the digestive system is composed of several membranous receptacles for the accommodation of the food, while a series of glandular organs furnish powerful secretions which are intended to simplify it. What is true of animals is also true of plants. Thus, the roots hold the plant firmly in the ground and are chiefly responsible for its nutrition, while the stem gives lodgment to the leaves in which certain chemical processes are effected under the influence of sunlight. The

flowers give rise to the fruits which embrace the seeds or reproductive elements.

This division of labor is evident even in the simplest organisms, such as the paramœcium. Its movements are evoked by the contraction of specialized filaments of protoplasm, the cilia, while its digestive function is instigated in an indentation of the integument, the gullet. Another specialized mechanism is the contractile vacuole which appears to subserve the movement of the intracellular material and excretion. Hence, even such simple protoplasmic entities as the protozoa are true organisms.

The Cell.—Whether protoplasm is organized to form a single free-living entity or a simple constituent of the tissues

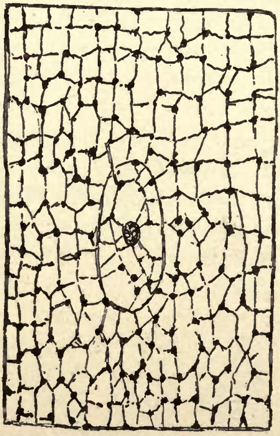


FIG. 1.—The structure of protoplasm. An epidermal cell of the earthworm. (*After Bütschli.*)

of the most complex animal or plant, it always presents certain structural and functional characteristics. A small particle of living matter possessing sufficient organization to be independently active, is known as a cell. Accordingly, it may be said that a cell represents the simplest type of individuality of living substance. It constitutes a unit in structure and function. As originally applied, the term protoplasm referred merely to the viscous ground-substance

of cells. We now know, however, that this constituent is quite unable to unfold its life processes unless mixed with certain other elements which are briefly designated as nuclear material. In analogy with the general conception that a cell is a walled space, similar in its outline to those forming the honeycomb or nests of certain insects, it has also been held that these fine globules of protoplasm are invariably surrounded by a delicate membranous capsule. This is not always the case, because such organisms as the amœba do

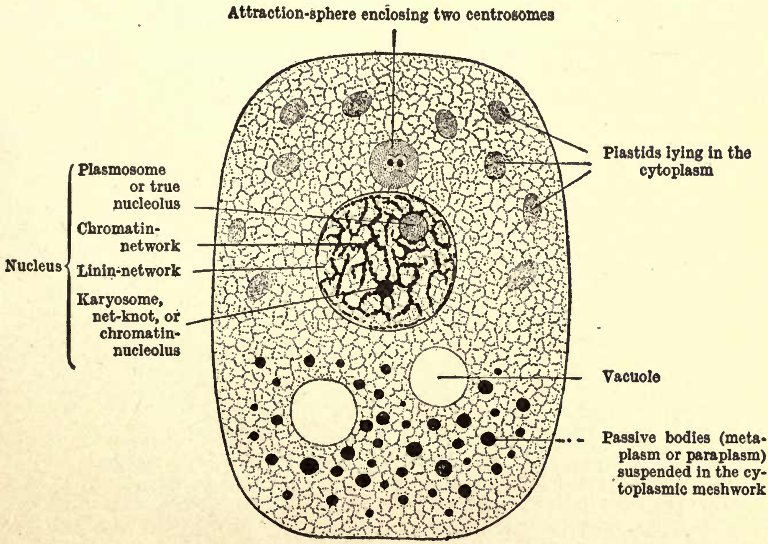


FIG. 2.—Diagram of a cell. (*Wilson.*)

not possess a distinct enveloping membrane. In the face of these still debated questions, it seems advisable to obtain first of all a clear conception of the structure of one of the more familiar types of cells, for example, of those composing the acini of the liver, pancreas, or salivary glands.

A cell of this kind is invested by a clearly differentiated wall, while its interior is occupied by a clear, homogeneous, viscous substance which is known as cytoplasm. Somewhere in this ground-material is embedded a dense, dark object,

generally rounded in outline, which is known as a nucleus. Within the latter is often found a still smaller globule of dark-staining material which is designated as a nucleolus. Under the low power of the microscope the ground substance exhibits a homogeneous watery consistency, which, however, becomes froth-like when subjected to high magnifications. Such a formation may be reproduced artificially by mixing

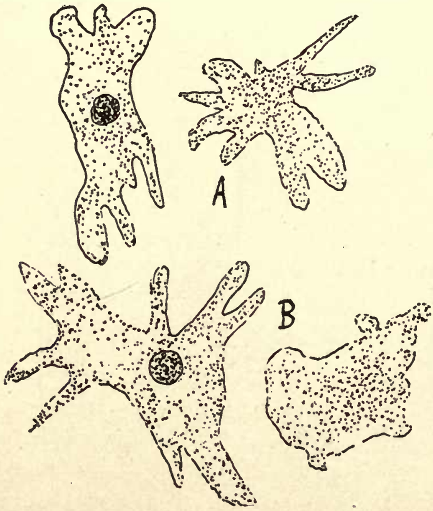


Fig. 3.—The functional relation of the cytoplasm and nucleus. *A*. An amœba divided into a nucleated and non-nucleated portion. *B*. The same portion after an interval of eight days. (*After Hofer.*)

a drop of oil with a small amount of cane sugar or potassium. All cells are said to contain nuclear material, although it may not always appear in the form of a sharply differentiated body, but as minute particles scattered through the cytoplasm. At all events, the nucleus is generally considered as being absolutely essential to the life of the cell, because any mass of cytoplasm which has been deprived of this constituent, soon loses its function and undergoes degenerative changes. This fact may be proved very easily by dividing an amœba into two parts in such a way that its nucleus is left entirely in one of these segments. The nucleated portion

regenerates very promptly, whereas the denucleated part soon ceases to move and to ingest food.

The cytoplasm of a cell also contains certain formed elements, representing material ready for assimilation and excretion. In addition, it may embrace certain accidental admixtures, such as pieces of shells and granules of sand. These admixtures are most easily recognized in the unicellular organisms which catch the particles of food by engulfing them.

The Chemical Composition of the Cell.—The chemical constitution of a cell cannot be ascertained during its life, because the analytical procedures employed at the present time bring its functional changes to a standstill. It should also be remembered that certain varieties of cells may contain a type of material which is not present in others. Such an inconstant constituent is the glycogen of the liver cell. But, disregarding these minor differences for the moment, it may be said that protoplasm contains about 75 per cent. of water and 25 per cent. of solids. Among the latter should be mentioned:

A. **Organic Material.** (*a*) *Proteins.*—These are the most constant and important constituents, and are present in the cytoplasm as well as in the nucleus.

(*b*) *Fats and Lipoids.*—Besides ordinary fats, protoplasm also contains certain substances which are soluble in alcohol and ether. They are known as lipoids. One of the most important bodies of this kind is cholesterol. When they embrace phosphorus, they are designated as phosphatides. Lecithin is the most important member of this group.

(*c*) *Carbohydrates.*—These organic substances are not found as original and free constituents of the cells. They may be present in glycoproteids and cerebrosides.

B. **Inorganic Material.** (*a*) *Water and Salts.*—As has just been stated, water constitutes about three-fourths of the entire bulk of protoplasm. In addition to the six principal elements mentioned above, it may also contain sodium, potassium, magnesium, calcium, iron, and at times even iodin, manganese, copper, zinc, barium, and silica. The proportion of these elements differs greatly in different cells.

The Size and Shape of the Cell.—Inasmuch as living matter appears either in the form of individual entities or as units of tissues, it may rightly be assumed that the size and shape of the different cells vary considerably. It may also be taken for granted that their fundamental shape is round, or nearly so, and that they become polyhedral only when combined with others to form larger masses. Likewise, it may be concluded that they cannot attain a very large size, because the ordinary physical forces do not suffice to hold

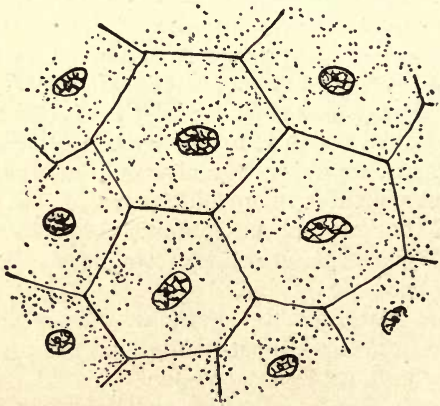


FIG. 4.—Epithelial cells in the web of the frog.

their substance together. By far their largest number remains below the range of ordinary vision, and very few attain dimensions that may be expressed in terms of millimeters (1). Furthermore, while no cell is absolutely dormant when living, they exhibit different degrees of motile power. Thus, it is evident that the cells forming the ordinary tissues and organs of our body are fixed, whereas the free-living cells, such as constitute the unicellular organisms, are capable of shifting their protoplasm and of moving from place to place. This form of movement which is characterized as amœboid, is most clearly betrayed by such organisms as the amœba and leukocyte. Again, many organisms consisting of only one cell, may move by means of accessory structures, such as flagellæ and cilia. These filamentous

processes are motile, while the principal mass of the cell remains inactive.

1. The unit of histological measurement is the micro-millimeter. It is indicated by the symbol μ. It will be remembered that a meter (39.3 inches) consists of 100 centimeters; and each centimeter (cm.) 10 millimeters (mm.) A micro-millimeter is the $1/1000$ part of a

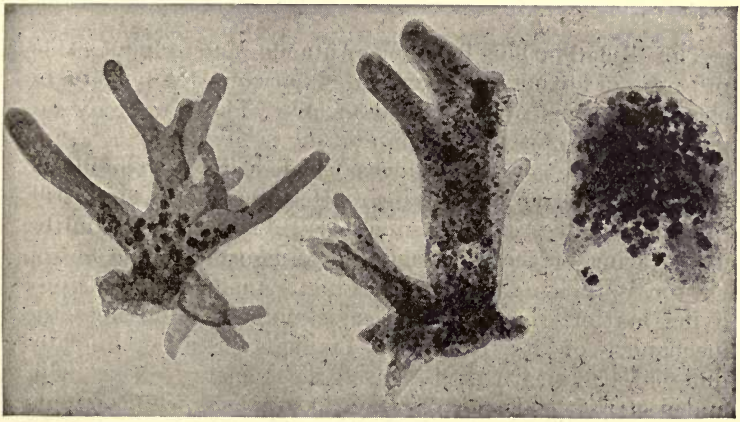


Fig. 5.—Amœba. (*From Calkins' "Biology," Courtesy of Henry Holt & Co., Publishers.*)

millimeter. Structures of so small a size must be subjected to microscopic vision in order to render them perceptible to the eye, a magnification of from 300 to 400 diameters being required to accomplish this end. But we also recognize in an indirect way certain active particles which cannot be seen even with the aid of a microscope. They are known as ultra-microscopic entities.

In order that the student may from a clear conception of these measurements, he should be in possession of a familiar object for comparison. For example, the shaft of a human hair possesses a diameter of 0.08 mm. or about $\frac{1}{300}$ of an inch. Likewise, the shaft of the hair from the fur of a rabbit has a diameter of 0.025 mm. which value equals about $\frac{1}{1000}$ of an inch. Its tip, on the other hand, measures only about 0.001 mm. or $\frac{1}{25000}$ of an inch. Accordingly, since the red corpuscle of the human blood is 7μ or 0.007 mm. in diameter, its cross-section would be about 7 times as large as that of the tip of a rabbit's hair.

CHAPTER II

GENERAL PHENOMENA OF LIFE

The Relationship Between Animals and Plants.—The processes of life may be investigated in two ways: namely, by chemical means and physical means. Thus, we may endeavor to discover the composition of living matter and attempt to detect the changes which arise therein in the course of its activities. Living matter is never at a standstill, but assimilates and dissimilates substances constantly. The tracing of these through the organisms is one of the chemical problems pertaining to life. Again, we may study living matter from the physical standpoint, and note the mechanics of its behavior. Living substance liberates different energies: namely, mechanical energy, heat, light, and electricity. To portray these in a realistic manner would be another way of ascertaining the cause and characteristics of life. But whichever method may be followed, it cannot yield favorable results unless amplified by the other.

We have been accustomed in recent years to regard organisms as mechanisms which act in accordance with definite chemical and physical laws. In other words, our study of the processes of life has been directed along mechanistic channels, whereas living entities were formerly regarded as unique in character, because they presented many as yet quite incomprehensible manifestations. This *vitalistic* view has not aided scientific progress very materially, because a conception which admits right at the start our impotence to cope with a certain problem, is by no means the most advantageous to select as a guiding principle.

It must be clearly recognized that matter is indestructible, and that all energy is conserved. Supposing that we are in possession of a certain inorganic substance which may be split chemically into its several components, we should not

assume that this substance is then absolutely lost. It merely assumes a different aspect for a certain period of time, and may again be built up into its original form later on. Furthermore, its components may severally enter new combinations. This *law of the conservation of matter and energy* is also applicable to organic material. Thus we find that the animals consume different complex substances which are reduced into their simple components and assimilated with liberation of definite forms of energy. They finally leave the body as waste products. Clearly, therefore, these substances are not lost but are merely transformed into simpler ones.

It is also apparent that a certain functional reciprocity exists between animals and plants, because the life of one sustains that of the other. This statement, however, holds true only for those species which one would naturally select for the purpose of illustrating this particular point, because certain varieties of plants, such as the fungi, are not in possession of coloring material, and are, therefore, quite unable to transpose material for fuel. In fact, the lowest living entities frequently present so similar a structure and function that one might be justified in classifying them either as animals or plants. A green plant is able to construct its complex material from the simplest substances, such as water, carbon dioxid, and different inorganic salts. An animal also requires certain organic material, although it is quite unable to form these from elementary inorganic substances. Consequently, the animal must acquire its fuel in a preformed state, and since the plants are capable of producing carbohydrates, fats and proteids from elementary substances, they become the most important source of nutritive supply to the animals. Thus, it may be said that the animals are the parasites of the plants, because their existence depends in a large measure upon the food prepared for them by the latter. As has been stated above, the fungi which contain no chlorophyl, are in a similar position, because they must derive their requirement of carbon from existing organic material.

It is evident that the plants are an essential factor in the life of animals. The reverse, however, is not true, because

water and inorganic salts are abundant in nature and carbon dioxid may be obtained from other sources than the expired air of animals. The excretory products of the animals, however, aid the plants at times in building up their substances. For example, it is a well known fact that the carbon dioxid emitted in the expiratory air of animals or as products of general combustions, is immediately made use of by the plants in their constructive processes. This synthetic power of the plants is of greatest importance, because it relieves the atmosphere of this admixture which if allowed to accumulate in considerable amounts, would eventually endanger the life of all animals. Again, the plants liberate oxygen which is inspired later on by animals, but this gas does not arise in the course of their respiratory processes, because plants inhale oxygen and exhale carbon dioxid. It is metabolic oxygen generated as a by-product during the formation of the complex constituents of the plants from simple substances. Sunlight and chlorophyl are the factors absolutely essential for this constructive process.

When regarded in a general way, it may be said that the plants form potential material for the animals, because they abstract simple substances from the earth and unite them into complex foodstuffs, such as the starches and the proteins. Plants are devoured by animals, and some animals in turn are devoured by others. These complex substances are then broken down by the latter under liberation of energy and are excreted; in fact, the animal as a whole eventually splits up into its simple components, permitting them to be again incorporated in the earth. Strangely one is here reminded of the words of Hamlet which read:

> "Imperial Caesar, dead and turned to clay
> Might stop a hole to keep the wind away,
> Oh that that earth which kept the world in awe
> Should patch a wall, to expel the winter's flaw."

This *transmutation of matter*, however, cannot be considered as being wholly constructive in the plants and destructive in the animals, because many animal tissues are capable of synthetizing simple substances into very complex bodies. For example, it is a well known fact that the proteins of

plants are broken down in the animal into their amino-acid constituents, and that these building stones are again united later on into the protein substances of the body. In many instances, these body-proteins are quite different from those ingested as food, but these syntheses are after all merely minor variations in the general process of the transformation of matter.

Oxidation.—Living substance is never in a state of complete inactivity. It grows; it moves; it secretes; and gives rise to various other changes which necessitate the production of energy. Where is this energy derived from? Evidently from a definite source within the protoplasm, because the substances entering into its composition undergo certain changes in the presence of oxygen. During these processes a certain form and amount of energy is liberated which renders the protoplasm dynamic. Contrariwise, any mass of protoplasm which is unable to instigate these changes, must cease being a living entity.

Oxidation, therefore, may be defined as a chemical union of oxygen with any other substance. Let me illustrate this statement by an example. A match is ignited by striking its head against a rough surface. The friction produced thereby causes the phosphorus, an element possessing a great affinity for oxygen, to unite with this particular constituent of the atmospheric air. In addition, the head of a match is usually covered with a layer of sulphur which combines with oxygen at a much higher temperature than phosphorus. Red lead, niter, and gum or glue are added to the impregnation fluid for the purpose of liberating oxygen at the beginning of this process and to bind all these substances together. Eventually the wood is ignited. The latter is composed in largest part of the element carbon, and undergoes a much slower form of oxidation than the other constituents of the match. During this process, a considerable amount of heat is evolved which may be made use of to produce work. Quite similarly, the oxidation of coal liberates heat which may be employed to boil water and to generate steam for mechanical purposes. This form of energy is the direct basis of work. Reference should also be made

at this time to certain oxidations which do not evolve an appreciable amount of heat. For example, if an iron nail is placed in a dish containing a small quantity of water, it will presently become covered with rust. This deposit is composed of iron oxide, a product of the union of iron with oxygen.

Inasmuch as carbon is the most important constituent of things that possess life, or organic material, the oxidations in cells must naturally strive to reduce the carbon combinations into simpler bodies. It is easily observed that the union of oxygen and carbon gives rise to a gaseous product which is known as carbon dioxid or carbonic acid gas. Another important component of organic matter is nitrogen, but this element is an inert gas and does not support combustions. The only other important constituent of such matter is hydrogen. When this gas combines with oxygen, water is formed. Thus, the burning candle liberates carbon dioxid from its carbon, and water vapor from the hydrogen of the wax. During these processes a certain amount of heat is evolved, its rate of discharge varying greatly with the character of the material.

Oxidation in Cells.—The destiny of living matter is to liberate energy and to produce work. In this regard it does not differ from any other material. The manner in which this end is accomplished is based upon a common principle, namely, that of oxidation. As in the cases of the match, coal and candle, the plants and animals cleave the complex substances with the liberation of carbon dioxid and water. This decomposition is as important to one as it is to the other, because it gives rise to an evolution of heat, and heat is the source of all forms of work.

What is true of protoplasm as a whole is true of the cells, whether free-living or combined with others into tissues and organs. Each is in possession of a certain store of material which it must burn up in order to fulfill its purpose in life. To be sure, the protoplasm of the different cells presents certain variations in its chemico-physical constitution. These differences between the cells lead to differences in their functional products. Thus, while one cell may furnish

mechanical energy in the form of motion, another may yield a secretion, but quite irrespective of their final products, the principle involved in these activities remains the same in all cases. Every cell must sacrifice its stored energy in order to live, although, correctly speaking, this decomposition cannot be called a sacrifice, because by following this path the cell merely fulfills the laws of the forces which created it.

Metabolism.—The constant liberation of energy by the cell must be compensated for. As living matter is unable to create its substances, it must get them from some external source, *i.e.*, from the medium in which it lives. Here various substances are held in readiness for it which it may acquire and utilize. All these substances contain energy, but energy in a resting or potential state. It becomes the duty of the cell to convert this potential energy into its dynamic or kinetic form.

This statement may lead us to infer that the cell cannot go on decomposing materials indefinitely. It must also acquire new substances to take the places of those destroyed. The former process is designated as dissimilation or catabolism and the latter, as assimilation or anabolism. Both together constitute the process of metabolism. Accordingly, it may be said that a cell is able to retain its position as the structural and functional unit of living matter only as long as its metabolic processes are rigidly controlled by it. A cell which in consequence of some inherent cause fails to metabolize, must cease its function and lose its value as a structural unit. But, naturally, this result may also follow an inability on the part of the cell to obtain a sufficient and proper store of materials from a medium which is in an impoverished condition. Although cells are capable of adapting themselves to environmental changes, their power of adjustment is limited and death must follow all variations of extraordinary character.

The manner in which cells acquire their nutritive material and discharge their waste products, differs in accordance with their general structure. Single organisms usually take them directly into their interior. Digestion and assimilation then follow. The multicellular organisms, on the

other hand, are in possession of special colonies of cells in the form of organs, to which the functions of ingestion and digestion are severally assigned. From the standpoint of the general tissue cells, digestion may be said to be extra-cellular, because the nutritive substances are brought to them completely predigested. The cells, however, are able to assimilate these simplified substances and to utilize them by virtue of a certain inherent chemical power. The same statement may be made regarding the excretory substances. The single free-living cells discharge their waste directly into the medium, whereas the more complex organisms are in possession of special organs which are set aside for the purpose of eliminating the useless material.

Food.—The conversion of potential into kinetic energy continues only as long as nutritive substances are available for purposes of assimilation and dissimilation. A substance which is instrumental in furthering the growth of the cell and serves as an aid in its oxidations to furnish energy, is designated as a food. This definition is sufficiently embracing to include water which to all intents and purposes is not a fuel, although it possesses a distinct value as a food. A similar difficulty arises in the case of the mineral salts which are necessary constituents of cells, but cannot singly be burned up to liberate energy. The proteins are not only essential constituents of the cells, but also give rise to energy on oxidation. Oxygen occupies a unique position, because it is not a fuel, but merely aids in converting certain substances into different forms so that it is possible to derive energy from them.

Not in complete analogy with the plants, the animals usually ingest mixtures of nutrient substances, such as are represented by potatoes, beans, peas, bread, butter, meat, etc. The substances which singly enter into the formation of a nutrient material, are known as food-stuffs. Accordingly, a food-stuff may be defined as a nutrient substance of definite chemical composition. The five food-stuffs which may enter into the formation of a food, are water, salts, carbohydrates, fats, and proteins. Thus, a potato may be said to contain several food-stuffs, for example, water, salts, carbohydrates in the form of starch, and a small amount of protein.

CHAPTER III

GENERAL CONDITIONS OF LIFE

Animate and Inanimate Material.—Inasmuch as physiology is the study of the dynamics of life, it seems advisable at this time to make brief inquiry into the characteristics presented by living matter. If the layman is asked to tell whether or not a thing is living, he first seeks to discover some evidence of motion, and if the latter is not forthcoming spontaneously, he touches the object in an attempt to call forth a reaction by stimulation. A scientific differentiation between inorganic and living organic bodies is usually made upon morphological, genetic, physical, and chemical grounds. It is usually stated that inorganic objects possess definite geometric proportions, while organic ones do not. This point, however, is not well taken, because organisms with geometric contours are not uncommon. Reference might be made at this time to the radiolaria, the calcarious envelopes of which are laid down along definite straight and curved lines. Upon genetic grounds it may be held that organisms always originate from organisms, but this difference remains real only if we adhere to the metaphysical conception of the origin of life and absolutely deny that it will ever be possible to produce living matter artificially.

It is also stated that living matter possesses the properties of irritability and contractility, while inorganic material does not. Let us take a small mass of gunpowder and spread it out in the form of a long and narrow band. On igniting it, an explosive reaction follows, during which the powder is progressively consumed. The amount of energy evolved during this reaction is infinitely greater than that liberated by any living organic material of equal size. Since our conception of irritability and conductivity is derived from the study of animal tissues, it may be somewhat difficult to recognize a distinct similarity between this process and those

taking place in the inorganic world. In reality, however, there is no difference unless it is one of generalities.

Chemistry tells us that living organic matter embraces certain bodies, the complexity of which greatly exceeds that of any inorganic material. Reference is had here more particularly to the proteins which only living matter is able to cleave and to assimilate. Even this difference will no longer be available after a way has been found to produce protein substances artificially. One difference, however, will always remain clearly recognizable and that is the specific metabolic function of living matter. Life requires a constant succession of metabolic changes involving complex organic materials. It is not possible to reproduce these with inorganic nor with dead organic material.

Peculiarities of Living Matter.—In a general way, it may suffice to state that living matter presents certain fundamental characteristics which may be classified under the following headings:

(*a*) *Irritability.*—The physical and chemical constitution of protoplasm is such that it permits outside influences to be received by it. These influences are absolutely essential to it, because they form the stimulus which keeps the intracellular machinery in motion. While this is a perfectly definite phenomenon, all inquiries regarding the nature or causes underlying this property of protoplasm must remain without answer, because the minute processes going on in cells are as yet not fully understood. From this brief statement it may be gathered that living matter must fail to function properly when these stimuli cease or when, in consequence of some inherent difficulty, it becomes non-receptive to them.

(*b*) *Conductivity.*—Whenever protoplasm is subjected to a stimulus, a local reaction follows which, however, does not remain confined to the locality first affected, but gradually spreads from here to its more distant regions. In this way, a wave of irritability or excitability is produced which extends in all directions through its mass. Some forms of protoplasm are more irritable and conductile than others. The tissue which shows these peculiarities in the most unmistakable manner, forms the nerves and their distal and central end-stations.

(*c*) *Contractility.*—The wave of excitation traversing protoplasm invariably gives rise to some sort of a reaction. This reaction is most plastically portrayed by motion. Inasmuch as protoplasm contains contractile material, a stimulus applied to it must cause it to shift its molecular constituents in such a way that the entire mass assumes a different shape and even moves from place to place. Clearly, a sharp distinction should here be drawn between the phenomenon of contraction as observed by physiologists and

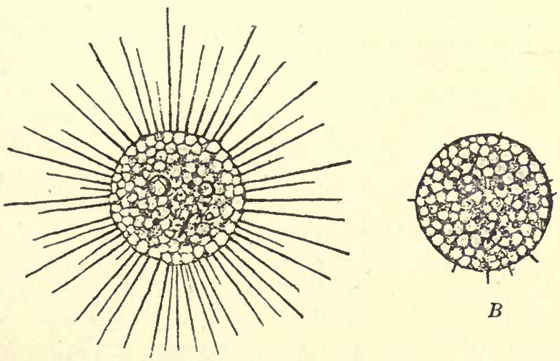


FIG. 6.—Actinosphærium. *A*, position of rest; *B*, position of stimulation. (*Verworn.*)

that noted by physicists. When an iron bar contracts in cooling, its volume is reduced in all directions. An organism contracting, however, merely changes its form and position, but cannot gain or lose sufficient material to change its volume.

(*d*) *Metabolism.*—It has been stated above that protoplasm cannot retain its fundamental characteristics unless constantly supplied with material from which it may derive a certain amount of energy. The liberation of this energy is accomplished by means of an elaborate series of mechanical and chemical processes.

(*e*) *Reproduction.*—Living matter is unstable. It decomposes but to recompose, and recomposes but to decompose. Hardly for a moment does it remain precisely in the same

condition. Besides, it undergoes gradual senile changes which eventually destroy it altogether. Even barring accidents, its life cycle is very brief. Scarcely has it fully unfolded its processes when it begins to retrogress and to show signs of impaired function. It follows that some provision must be made for the replacement of these senile living entities by new ones, otherwise life upon the earth would soon become extinct. Nature has taken all possible precautions to protect living matter against such an eventuality. The perpetuation of the species is its highest law which it defends with a perfectly amazing prodigality.

The function of reproduction should be clearly distinguished from growth and regeneration. Whenever the ingo exceeds the outgo, the organism accumulates material. It grows and its weight increases. This formation of storative protoplasm out of the food is most intense during the early periods of the existence of the organism. Somewhat later an accurate balance is established, which finally gives way to an increased expenditure and corresponding shrinkage of the protoplasm. It may also happen that an organism loses one of its parts entirely. In many instances this part may again be reformed. The processes of growth and regeneration, however, invariably concern one and the same organism and possess no direct bearing upon the formation of entirely new entities to take the places of those destroyed.

The Phenomenon of Stimulation.—Every cell, whether leading an independent existence as an organism or combined with others to form the tissues of the higher plants or animals, is composed of certain substances which are made to interact and to liberate energy. The question may now be asked whether these processes are perfectly spontaneous or whether they are set in motion by some outside force. Let us observe for a moment an amœba as it moves from place to place seeking its sustenance. It sends out its pseudopods in one particular direction, meanwhile retracting its protoplasm elsewhere, until it comes in contact with a nutritive particle, such as a diatom. This it gradually surrounds until it assumes a position in its interior near its posterior pole. In this way a food vacuole is formed which consists of the

diatom and a small quantity of water. The amœba continues on its way, seeking other prey. Meanwhile the engulfed organism is slowly dissolved. If it contains coloring matter, this is changed to a brown color in consequence of oxidation. Nothing is left of it after a time excepting the pieces of its calcareous shell, and these are finally deposited in the wake of the amœba. Obviously, the protoplasm of this free-living cell possesses the power of converting the substance of its prey into a soluble and diffusible form, so that it may be embodied in its own mass.

In what particular, we may now ask, does the behavior of the higher animal differ from that of the amœba? The answer no doubt will be that the principle involved is absolutely the same, although certain differences are apparent which are not of fundamental importance. In whatever form living matter may appear, it is constantly subjected to outside influences which affect it in a perfectly definite manner. In consequence of these influences, it must execute certain reactions, because only when its behavior is made to conform precisely to the forces in the universe can it continue to manifest its processes of life efficiently.

This point may well be illustrated with the help of a concrete example, such as is presented by the activity of the heart. It is a remarkable fact that this organ will continue to contract after it has been removed from the body and has been placed in a dish under proper conditions of moisture and temperature. Apparently, its action is quite spontaneous, because it seems to take place without any tangible external cause. Such movements, instituted in response to an invisible stimulus, are characterized as automatic. In reality, however, this "spontaneity" is the result of the action of stimuli in the form of certain salts which cause the contractile elements of the heart muscle to undergo very characteristic reactions. What is true of the heart is also true of other tissues and organs. Consequently, it may be concluded that life is possible only in the presence of definite exciting agents or stimuli which cause living matter to manifest those responses for which it is peculiarly fitted by virtue of its structure and composition.

Manifestations of Energy.—Living matter is found in the air as well as in the water. Both media are teeming with different forms of energy which in general may be classified as vibratory and chemical, and embrace the following impacts:

(*A*) **Vibratory Energy.**—(*a*) Mechanical impacts of different quality and frequency.

(*b*) Vibrations in material media, such as air and water. They are slow and give rise to the sensation of sound. Special sense-organs are set aside for their reception, for example, the organ of Corti in the internal ear of the mammals. The human ear is capable of receiving vibrations in air varying between 30 and 30,000 in a second. The range of the well-trained ear is even greater than this, namely, 50,000 in a second.

(*c*) Vibrations in immaterial media, such as ether which constitutes a peculiar medium occupying space together with the air. The vibrations in ether vary between 3000 and 6,000,000,000 in a second and give rise to the so-called electrical waves, heat-rays, light-rays, Roentgen-rays, and others.

(*B*) **Chemical Energy.**—Chemical impacts are caused by a large number of substances. Upon the lower forms their action is direct, whereas the higher animals receive them, as a rule, through special organs, such as the taste-buds and olfactory cells. The former mediate the sense of taste, and the latter, the sense of smell. A special chemical sense evoked by certain end-organs of the skin is present in many organisms. Since osmotic changes in the surrounding medium are usually associated with chemical reactions, they do not merit separate enumeration.

Classification of Stimuli.—It should be clearly understood that phenomena of stimulation result only when the force or character of the impacts acting upon living matter is suddenly altered. Accordingly, a stimulus may be defined as any extraordinary change in the environment in which the organism is living. We have seen that the energies in space are very diversified, and that any particular plant or animal may be more receptive toward one impact than

another. In fact, some of these energies may fail altogether in evoking a reaction in certain types of organisms, because the latter have no means of receiving them. Thus, a sound-wave is quite unable to produce a typical effect in amœba and allied organisms unless possibly as a simple mechanical impact after it has been transferred into vibrations of water.

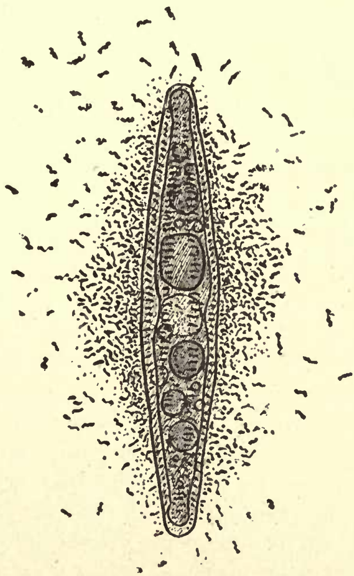


FIG. 7.—Diatom liberating oxygen attracts numerous bacteria. (*Verworn.*)

Every organism is constantly subjected to particular types of stimuli, and only in the presence of these can it fully unfold its life processes.

The character of the stimuli to which living matter may be exposed is very diversified. In spite of this fact, however, it is possible to arrange them in the following order:

(*a*) *Mechanical.*—In this group belong such stimuli as touch, pressure, stroking, pulling, the forces of gravitation, adhesion and cohesion.

(*b*) *Chemical.*—Various substances possessing either a favorable or an unfavorable influence upon living matter, belong in this group of stimuli. In addition, mention should be made of those excitants which are the direct result of osmotic interchanges.

(*c*) *Thermal.*—These stimuli originate in changes in the temperature of the medium.

(*d*) *Photic.*—Light is a very potent and valuable stimulus. Besides the ordinary rays, living matter may also be subjected to particular types of ethereal vibrations, such as produce the Hertzian heat rays or the Roentgen rays.

(*e*) *Electrical.*—Phenomena of stimulation also result when living matter is exposed to the electrical current. Magnetic stimuli do not merit special enumeration, because it is doubtful whether they are able to influence living matter directly.

The Strength and Duration of Stimulation.—In rating the effect of a stimulus attention should be paid to its quality as well as to its strength, the latter term serving as an expression of its intensity, duration, and frequency. Living matter exhibits the most efficient reactions when the stimuli acting upon it possess a moderate duration and strength. At this time *optimum* conditions are said to prevail towards which it reacts in an optimum manner. But, stimuli may also increase in intensity, becoming first *maximal* and later on *supramaximal* in character. Toward the former, living substance responds by increasing the amplitude of its reactions, but, naturally, a maximal activity cannot be endured for any length of time and must finally prove injurious to it. Supramaximal stimuli are destructive from the start and quickly result in the death of living matter.

Lastly, the intensity of the stimuli may be so slight that they fail to excite living matter in a proper manner. These *minimal stimuli* evoke minimal responses. On reducing the strength of the stimuli still further, a point will eventually be reached when the stimulus just barely produces a reaction. This is the *threshold value of the stimulation* at which the slightest possible reaction is obtained. Below this point, the stimuli must fail to excite living substance in an appreciable manner. To be sure, these *subminimal* stimuli may

produce certain chemico-physical reactions in protoplasm, but their strength is not sufficient to induce a visible response. Obviously, life is impossible under these circumstances.

It is to be noted, therefore, that death ensues whenever the realm of stimulation is extended beyond its minimal or maximal limits. It should be remembered, however, that optimum conditions are not always found strictly midway between these two extremes. Protoplasm differs considerably in its constitution, so that stimuli possessing an optimum strength for one type, may not be equally effective for an-

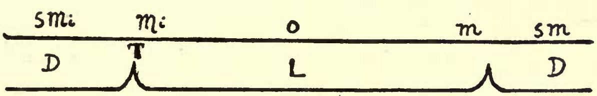


FIG. 8.—Intensity of stimulation. *L*, life; *D*, death; *SMi*, subminimal; *Mi*, minimal; *O*, optimum; *M*, maximal; *SM*, supramaximal stimuli; *T*, threshold.

other. Thus, the temperature of the Arctic Ocean may be quite suitable for certain organisms, but very destructive to others.

Living matter also possesses the power of adapting itself to stimuli. Thus, a certain influence which at first produces a considerable response, may in the course of time become quite ineffective. This state of *adaptation* presents certain similarities to the state of *refraction,* although the latter possesses an entirely different cause. We have seen that every activity of protoplasm is associated with a certain loss of material, and that the substances destroyed must first be rebuilt before another response can be given. Consequently, too rapid a succession of stimuli must be connected with certain dangers to function, because it does not allow the protoplasm sufficient time in which to acquire new material in preparation for the succeeding reaction. A point will then be reached when the succeeding stimuli must fail to evoke responses. The interval which protoplasm absolutely requires for its anabolic processes and during which it remains, so to speak, impermeable to stimuli, is designated as the *refractory period.*

SECTION II

MUSCLE AND NERVE

CHAPTER IV

MOTION

The Arrangement of the Subject-matter.—Physiology deals with the functions of the organism. It informs us regarding the uses to which the different parts of the latter are put in order to obtain a co-ordinated living whole. But, even the lowest forms allow us to infer that their behavior is the product of several functions, although the simpler the living entity, the more rudimentary are the activities of its different component parts. Thus, it is a relatively simple matter to study the movements of the amœba, paramœcium and allied organisms, but very difficult to analyze their methods of respiration, metabolism, and excretion. We know that these functions must be present, because without them they could not exist. This division of labor is more apparent in the higher forms, in which we are able to recognize special groups of organs, each fulfilling a definite function, and all combined imparting to the organism as a whole a definite general behavior. One complex of organs attends to motion and locomotion, another to respiration, another to the assimilation and dissimilation of the food, another to excretion, another to the distribution of the assimilated material, another to the co-ordination of all these functions, and still another to reproduction and the propagation of the species.

This division of function makes it possible for us to approach the subject of physiology in an analytical manner. Somewhat in accordance with the methods practiced in the

dissecting room, the gross function of an organism may be separated into its minor contributory functions, and having obtained these single parts, we may again fit them into one another in an endeavor to observe the working of the whole. The most concrete subjects of physiology are those which deal with motion and locomotion, the circulation of the blood, the interchange of the gases, the assimilation and dissimilation of the food, and the nervous control of these functions. While these subjects permit of a different arrangement, it is advantageous to place motion first, because it is most easily understood and introduces the student to physiology, so to speak, through the channel of least resistance.

Different Types of Motion.—By virtue of its property of irritability, protoplasm is able to receive stimuli and to liberate in consequence of them certain forms of energy, such as mechanical work, heat, and electricity. The mechanical form of energy is based upon motion and locomotion. These manifestations of protoplasmic activity present themselves either as passive or active movements, the very diversified character of which is due to differences in the shape and size of the organs producing them. A movement may follow any one of the changes enumerated in the succeeding table:

Motion	A.—Passive, due to the dynamic condition of matter, because its molecules are always moving.		
	B.—Active	Swelling of the cell wall	
		Changes in the cell-turgor	
		Changes in the specific gravity	
		Secretion	
		Growth	
		Contraction and Expansion	amœboid ciliary muscular

A *passive* movement follows the impact of an outside force upon a movable object. If we observe the circulation of the blood in the web of the frog, the different cellular elements of this fluid will be seen to traverse the vessels with a definite velocity; however, their progress is not due to an activity of their own but to an outside force resident in the pumping action of the heart. Active movements result, for example,

in consequence of the *absorption of water* by an expansible body. If a dry, wedge-shaped piece of wood is placed between two stones and is allowed to imbibe water, it gradually increases in volume and presently forces the stones apart. This type of motion is most plastically portrayed by the so-called resurrection plants of desert regions. When dry, these plants possess the appearance of crumbled-up filaments of leaf, while in a moist atmosphere they unfold their parts and assume more definite shape.

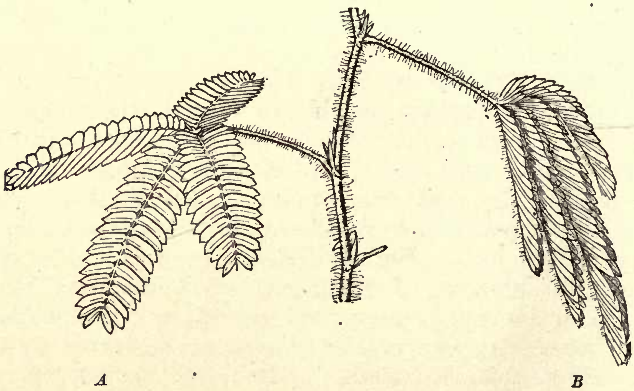


FIG. 9.—Sensitive plant (Mimosa pudica). *A*. Resting position. *B*. Stimulated. (*Verworn after Detmer.*)

A very interesting movement is brought about in certain plants by *changes in the turgor or tension* of the cells. Owing to rapid osmotic interchanges and the contraction of the primordial sac, the elastic wall of the cells is made to fluctuate. In the so-called sensitive plants this movement is very sudden and may be evoked by different stimuli. Merely touching a plant of this kind (mimosa pudica) causes it to close up its leaflets and to droop its stems. A similar reaction occurs when the intensity of the light is lessened. In this group also belong the common bladderwort, Venus' flytrap, and certain pitcher plants. The apical portions of the leaves of these plants are modified to form pouches which are beset with hair-like projections. These hairs are directed downward and are sensitive to stimuli. The slightest touch causes

the leaf to close along the midrib, thereby entrapping its prey. The leaf contains many glands which then pour forth a secretion capable of digesting diverse nitrogenous materials by virtue of a particular proteid-splitting enzyme.

Movements by *changes in the specific gravity* of the organism are most convincingly betrayed by the radiolaria. Ordinarily heavier than water, these cells live upon the bottom of stagnant pools. They rise to higher levels in consequence of the

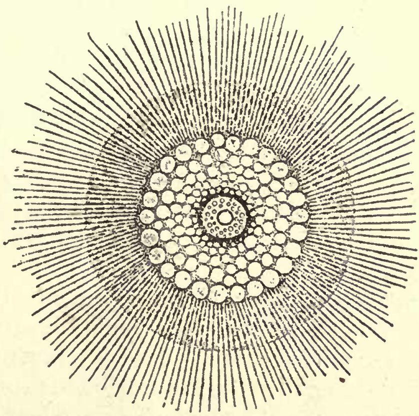


Fig. 10.—Radiolaria cell showing central nucleus and zone of vacuoles surrounding it. (*Verworn.*)

deposition of bubbles of metabolic carbon dioxid among their radiate prolongations. Their downward movement begins immediately after these gaseous formations have been broken up in the agitated layers near the surface of the water.

Movements by *secretion* may be studied in algæ and oscillariæ. These organisms project a sticky material from their bodies which aids them in gliding from place to place. Movements by *growth* are very common but usually very slow. Much more rapid movements of this kind may be elicited from the seeds and fruits of many plants. Thus, it is a matter of common experience that the touching of certain seeds causes their capsular investments to burst in consequence of the high degree of tension stored up within their substance.

Among animals the most striking movement is accomplished by means of protoplasmic *contraction and expansion.* Owing to the presence of a certain amount of contractile material within their protoplasm, they are able to assume a more compact and rounded form when stimulated. This state is followed sooner or later by that of expansion or relaxation during which the entire mass becomes flatter and larger in size. Contraction signifies stimulation, whereas relaxation indicates rest and the absence of stimuli. In this connection, we should recall to our minds the mode of progression of amœba and allied organisms, which exemplifies the so-called amœboid movement. But, in many instances, the main mass of the organism remains rather immotile, while it as a whole is moved onward by certain accessory structures, such as cilia, flagella, and muscles. Inasmuch as these contractile elements are present in all the higher forms, it seems advantageous to study them with at least a fair degree of detail.

Amœboid Motion.—The amœba represents the simplest form of life, because it consists of a single bit of protoplasm. It does not possess a fixed shape, but is constantly shifting its mass, thereby enabling it to send out delicate processes in one direction and retracting its substance elsewhere. In doing this it will be noted that its granular central portion or endoplasm is moved less easily than its outer hyaline zone or ectoplasm. No definite part of this cell is set aside for the reception of food, although it usually moves about in such a way that these nutritive particles come to lie in its posterior portion. Like other cells it takes in oxygen and discharges carbon dioxid, liberating in consequence of these oxidative processes a definite amount of energy. How this end is accomplished is not known, because this organism is altogether too small to be able to observe these changes directly.

The type of movement displayed by amœba is not restricted to this particular form, but is also exhibited by the rhizopods, egg cells, pigment cells, giant cells, and the leukocytes of the higher animals. The leukocytes make use of their power of amœboid motion in engulfing foreign material which has entered the blood or tissues. This they

digest and render inert, thereby protecting the body against injury

Ciliary Motion.—Many free-living cells move by means of one or two long threads of protoplasm protruding from one pole of their body. These filaments are known as flagella. When contracting they swing into a position next to the sides of the cell-body, thereby forcing the latter forward. A very similar motile mechanism is furnished by the cilia

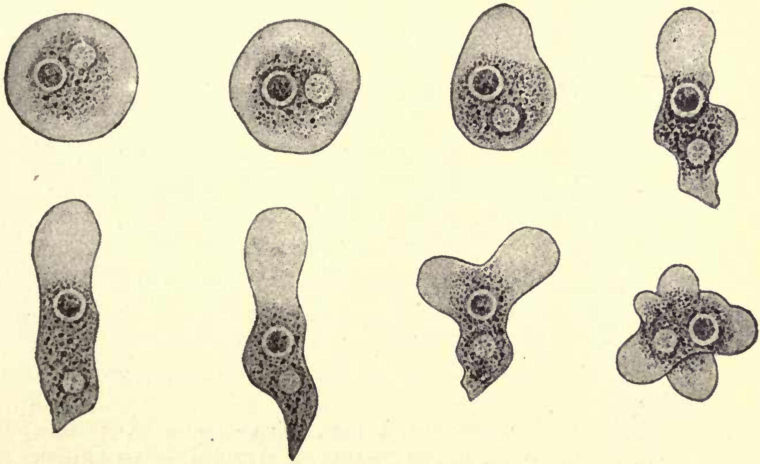


FIG. 11.—An amœba, showing different stages of movement. (*Verworn.*)

which present themselves as short hair-like processes projecting in great numbers from the surface of the cell. The action of these protoplasmic filaments may be studied with advantage in certain protozoa, such as the paramœcium or slipper animalcule. When placed under the ocular of a microscope, this organism will be seen to possess an elongated, oval outline, one of its poles being more pointed than the other. Its surface is everywhere beset with delicate hair-like processes which contract at regular intervals and in a definite direction, thereby lashing the water like tiny oars and causing the cell as a whole to progress in a direction opposite to their stroke. This unicellular organism possesses

a higher organization than amœba, because the particles of food reach its interior through a funnel-shaped depression in its surface and appear later on as food-vacuoles inside its protoplasm. In addition, this organism exhibits contractile vacuoles which pulsate at regular intervals and appear to play the part of excretory and circulatory organs.

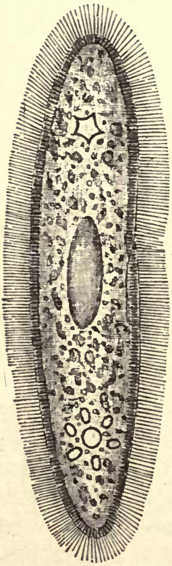


FIG. 12.—Paramœcium, a ciliated infusorium.

Cilia are widely distributed throughout the animal kingdom. In the higher forms they appear upon the free surfaces of the cells lining the respiratory and digestive tracts, as well as upon those lining the uro-genital passage. In man, we find them upon the mucous membrane of the nasal passage, lacrimal duct and sac, Eustachian tube and tympanic cavity, upper portion of the pharynx and larynx with the exception of the vocal cords, trachea and bronchi, Fallopian tube, vagina, central canal of the spinal cord, and the ventricles of the cerebrum. During embryonal life they are also present in the mouth, esophagus, and stomach.

The cilia found in the trachea of man measure only 0.003 to 0.005 mm. in length and 0.0003 mm. in thickness. Much better preparations may be obtained from the mucous lining of the mouth of the frog or from that of the gill-plates of the clam. If a piece of one of these membranes is placed under the ocular of a microscope, so that its edge is brought into view, it will be noted first of all that the water next to the surface is moved in the form of a definite stream. The small particles suspended therein proceed in the same direction, being abruptly projected onward whenever they come in contact with the lining cells. On closer observation we may then make out the individual cilia, forcibly striking in a particular direction and again bending back into their original positions. Inasmuch as each cilium is firmly anchored with

its basal portion in the marginal zone of the lining cell, it executes a movement in a definite plane, becoming sickle-shaped while contracting. This movement constitutes its *effective stroke.* When relaxing the cilium moves in the reverse direction until it has again assumed a position almost parallel to the surface.

Since a ciliated infusorium is equipped with many thousands of these cilia, and even a single lining cell may be beset

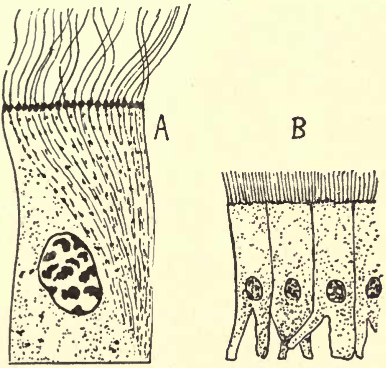


FIG. 13.—Ciliated cells. *A*, from a liver duct of the garden snail; *B*, from mucosa of frog. (*After M. Haidenhain.*)

with several hundreds of these contractile projections, the question may be asked how these structures can avoid striking against one another. It is to be noted that the different rows of cilia contract successively, those in the first row always being in a more complete state of contraction than those in the second, and so on until the last line has been reached. In this way, the entire ciliated area is divided functionally into several smaller ones, simulating somewhat the effect produced by a gust of wind as it strikes a field of wheat.

The question may also be asked whether the action of these different rows of cilia is co-ordinated by nerve fibers. Inasmuch as the existence of such fibers has not been proven and seems, moreover, very unlikely, we must conclude that

the cilia are able to influence one another by simple protoplasmic continuity. It is also of interest to note that a reversal of the effective stroke of the cilia has been observed in certain organisms. In the sea anemone, for example, the cilia around the edge of the mouth usually beat from without inward, thereby directing a steady stream of water into the body-cavity. If, however, a non-nutritive substance, such as a granule of sand, is placed upon the oral margin, the cilia reverse their beat in an endeavor to expel this foreign particle.

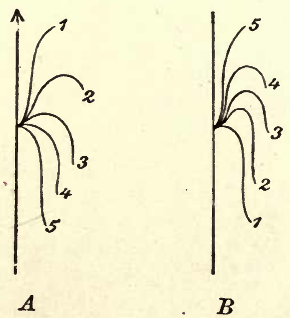


Fig. 14.—Movement of a single cilium. *A*, Progressive in direction of arrow; *B*, Regressive. (*After Verworn.*)

Since the contraction of each cilium is executed somewhat after the manner of a whip when lashed, it must be evident that any particle coming in contact with it must be projected in the direction of its effective stroke. This fact may be illustrated by placing a few bits of cork upon the exposed mucous lining of the frog's mouth. These particles will then be seen to move in the direction of the esophagus and, if the latter has been laid open, into the stomach. In the adult mammal, the lining membrane of the digestive tract is non-ciliated throughout. Cilia, however, are found in the respiratory passage, where they beat towards the outside. Their function is to move the particles of dust into the pharynx, whence they are flushed into the stomach by the saliva. It is true, however, that a certain proportion of dust always gets beyond these ciliated regions into the finer bronchioles

and alveoli of the lungs. Thus, the domestic animals and inhabitants of the cities commonly present lungs considerably stained with coal dust. It is true, however, that a much greater amount of this foreign material would be able to enter if these tubules were not ciliated. Particularly heavy depositions of dust are frequently found in the lungs of coal miners and marble cutters. Nature eventually

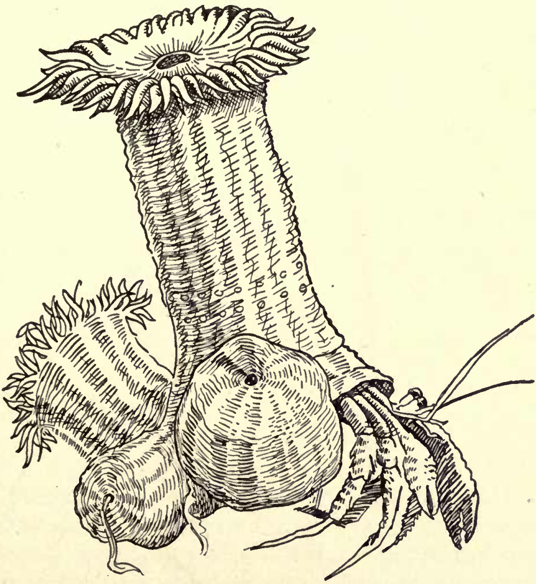


FIG. 15.—The sea anemone.

endeavors to dislodge them by a catarrhal inflammatory reaction which may at times assume the general character of tuberculosis.

Muscular Movements.—Besides the protozoa or one-celled entities, the animal world also embraces many-celled organisms or metazoa. The latter group presents a much higher type of motion than the former. This change is dependent upon the development of a more complex tissue which is designated as muscle tissue and is made up of cells possess-

ing an extraordinary contractile power. This statement, however, is not meant to imply that amœboid and ciliary motions are absent in the higher forms. Neither should it be interpreted as suggesting that muscle cells are not found in the lower forms, because several infusoria exhibit in certain

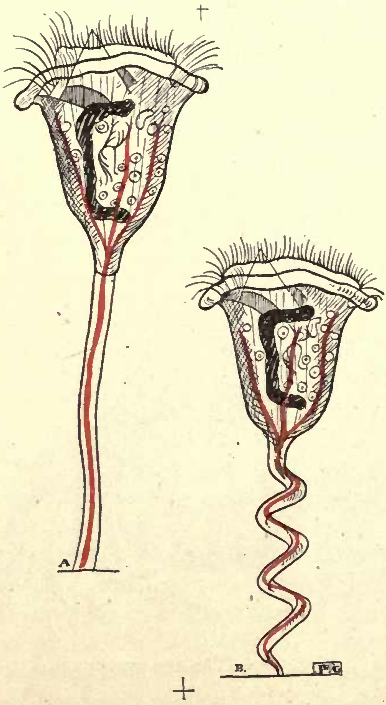


FIG. 16.—Vorticella in the resting position (*A*) and position of stimulation (*B*). The myoids are indicated in red.

parts of their protoplasm long fibrillar structures which shorten on stimulation, thereby causing the length of the entire organism to be instantaneously diminished. But, these fibrils are not identical with the muscle cells of the mammals, although it must be admitted that they present certain similarities in structure as well as in action. They are usually designated as *myoids*.

In the organism known as stentor, these contractile elements appear as single filaments below the envelope of its trumpet-shaped body, whereas in vorticella they are united into a bundle which occupies the stalk upon which the bell-shaped upper portion of its body is situated. During moments of non-stimulation either one of the organisms just mentioned extends its oral pole far into the water, permitting the cilia upon the margin of its mouth-cavity to divert particles of food into its interior. When stimulated, its head-end is swiftly retracted toward its basal portion which serves as the point of attachment for the organism as a whole.

Broadly speaking, it may be stated that these myoids are the precursors of the muscle cells of the higher animal. They pass through several evolutionary stages, giving rise first of all to the so-called smooth muscle cell and eventually to the striated muscle cell. A type somewhat different from these is the cell of the cardiac muscle tissue. When observing a higher animal, we note that it moves from place to place by means of large masses of muscle tissue which are attached to its bony framework. The constituents of the latter are employed as levers to increase their power. This type of muscle tissue is characterized as *striated*, because its cellular components present distinct cross-striations when studied with the aid of the microscope. It is also designated as *skeletal muscle tissue* and as *voluntary muscle tissue*, because it is attached to the bony framework of the body, and is under the direct control of the will. This statement implies that the contraction of every striated muscle is instigated by impulses which are conducted to it from nerve cells situated in a particular region of the central nervous system.

Besides this general movement of locomotion, an animal of this kind also exhibits certain movements of its internal organs or viscera. Its stomach and intestines contract upon the ingested material, reducing it in a mechanical way. Its bloodvessels constrict, thereby varying the size of its vascular channels. Its urinary receptacle contracts at definite intervals in an attempt to expel its contents. These internal movements are accomplished by means of *smooth muscle cells* which are embedded in the connective tissue

framework of these organs. They are characterized as smooth or plain, because they do not present a striated appearance in microscopic vision, and are, therefore, most closely related to the myoids. In other words, smooth muscle is a more primitive type than the striated variety. Inasmuch as these cells are found chiefly in the viscera, they form what might be termed the *visceral muscle tissue*. Moreover, since the movements observed in these internal organs are not under the control of the will, this tissue may also be characterized as *involutary muscle tissue*. This statement implies that the nervous impulses which activate it, originate in nerve centers which are not dominated by volition.

The *muscle tissue of the heart* presents a structure somewhat different from that of the preceding ones. In addition, it may easily be noted that its activity is not the result of external stimuli, although it is a well known fact that internal stimuli of some sort are at work to make it contract. A tissue which continues to react rhythmically without any apparent external cause, is designated as an *automatic* tissue.

CHAPTER V

THE STRUCTURE AND GENERAL BEHAVIOR OF MUSCLE TISSUE

Smooth Muscle Tissue.—If we examine an organ such as the stomach, intestine, or ureter, we find that it is made up of several of the four principal tissues. Its supporting web consists of connective tissue cells, in which are embedded varying numbers of smooth muscle cells. The latter are usually arranged transversely as well as longitudinally to the long axis of the cavity of the organ. The circular layer is situated as a rule next to the epithelial lining or mucosa, while the longitudinal one lies close to the external membranous covering of the organ. Besides, an organ of this kind always contains nerve fibers and nerve cells which regulate its function, as well as bloodvessels and lymphatics subserving its metabolic requirements.

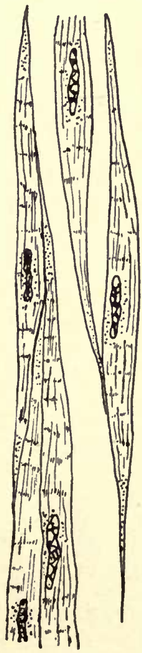


FIG. 17.—Smooth muscle cells, teased apart and showing long oval nuclei surrounded by undifferentiated protoplasm.

Smooth muscle tissue, therefore, consists essentially of a sheet of connective tissue moulded to form a tube and equipped with varying numbers of smooth muscle cells. The internal surface of this tube is lined with epithelium, while its external surface is covered with a layer of thin plate-like cells. Inasmuch as large numbers of these smooth muscle cells are arranged circularly around the lumen of the tube, their contraction must give rise to a diminution in the size of the latter. This particular point may well be illustrated by a brief study of the character

of the movements occurring along the intestinal canal. At the height of digestion, waves of constriction are seen to progress over it which are commonly designated as peristaltic waves. Every one of these waves consists of a zone of constriction which is preceded by a zone of relaxation. In this way, the contents of the canal are forced onward in the direction of least resistance. It is to be noted, however, that these movements are participated in by both layers of muscle cells, the circular one as well as the longitudinal.

The manner of action of these contractile elements may also be observed in the iris, a membranous diaphragm or stop situated in front of the lens and between the anterior and posterior chambers of the eye. It is a matter of common knowledge that the size of its central orifice, the pupil, is changed repeatedly in accordance with the intensity of the light. This reaction is made possible by numerous smooth muscle cells which are arranged either circularly around the pupil or radially to it. On contraction of the former layer, the margin of the iris is moved inward, thereby diminishing the size of this orifice. A smaller bundle of light rays is then permitted to enter the interior of the eyeball. Contrariwise, the contraction of the radial cells retracts the margin of the iris, thereby increasing the size of the central opening. At this time a larger number of light rays is allowed to reach the interior of the eye.

When one of these muscle cells is examined under the microscope, it is found to possess a spindle-like shape and a length varying in different organs between 45 and 225μ (average: $\frac{1}{500}$ of an inch). Its breadth varies between 4 and 7μ (average: $\frac{1}{4000}$ of an inch). The nucleus occupies a central position and exhibits a long-oval shape. The cytoplasm presents a delicate longitudinal striation.

Striated Muscle Tissue.—When examining a skeletal muscle, such as the gastrocnemius, it will be found that it is enveloped by a sheath of connective tissue which is called the perimysium. A large number of membranous partitions proceed inward from the inner surface of this envelope,

subdividing the space within the perimysium into numerous smaller compartments in which the individual striated muscle cells are situated. Each cell is surrounded by a wall or sarcolemma, neighboring cells being cemented together by a small amount of intercellular substance.

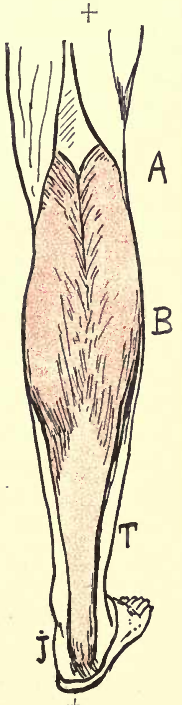


FIG. 18.—Gastrocnemius muscle. *A*, Attachment; *B*, body, consists of two halves; *T*, Tendo Achillis; *I*, insertion into calcaneum or heel-bone.

A muscle of this kind presents three principal parts: namely, a point of attachment, a body, and a point of insertion. The upper pole of such a muscle invariably contains fewer muscle cells, and its connective tissue is modified to connect it firmly with the bone. Below this *point of attachment* the muscle cells greatly increase in number at the expense of the connective tissue. This portion of the muscle is known as its *body* or *belly*. Below this level the connective tissue again increases in bulk, gradually displacing the muscle cells. Finally, a slender *tendon* is formed which is securely fastened to the periosteal lining of a freely movable bone. This constitutes its point of *insertion*. Everywhere else the muscle is related to neighboring structures through the medium of loose *fascia*, an extensive net-work of connective tissue. The blood vessels and nerves traverse its interior by following the partitions of connective tissue.

Contrary to the smooth muscle cells, the striated cells are united into compact masses which are fastened to different parts of the skeleton without consuming an unusual amount of space. By far the largest number of these muscles is concerned with the process of locomotion which, after all, is a most important function, because upon it depends practically the only means which the animal possesses to obtain its food. It should be remembered, however, that several of the skeletal muscles are related to locomotion only in an

indirect way; for example, those of the abdominal wall which are primarily intended to form a flexible covering for this cavity and to help in keeping the body erect. Still farther removed from locomotion are those which bring the lower jaw against the upper, and those initiating the act of swallowing. Even several of the respiratory muscles are not directly concerned with locomotion.

It is also of interest to note that the general arrangement of the cells is not the same in all muscles, a point which may readily be proved by a comparison of the sartorius and gastrocnemius muscles. The former possesses a long and slender shape, and its components are arranged practically parallel to one another. A muscle of this kind is not very powerful, but is able to lift a weight to a considerable height. Contrariwise, the gastrocnemius which is the chief calf muscle, possesses great strength, although it is unable to shorten very materially. This peculiarity in its behavior may be ascribed to the fact that it is built up around a strong core of connective tissue from which the individual muscle cells extend in an oblique direction downward and outward, finally terminating in its thick outer investment. On contracting, these cells pull upon this connective tissue capsule which in turn lifts the tendon of Achillis and extends the foot upon the leg.

If a stained preparation of striated muscle tissue is placed under the ocular of a microscope, it will be noted immediately that its individual cells are relatively long and thin. For example, those composing the sartorius muscle of the frog may attain a length of 3 to 4 cm., but a diameter of only 1 to 10μ (average: $\frac{1}{400}$ of an inch). For this reason, they are generally designated as fibers. Their ends are somewhat pointed and are joined with others in series by intermediary strands of connective tissue. If one of these cells is observed under the high power of a microscope, it will be seen to be invested by a wall or *sarcolemma,* underneath which are placed several nuclei in series. The interior of each cell is occupied by contractile material which exhibits alternate dark and light bands, similar to a glass rod which has been

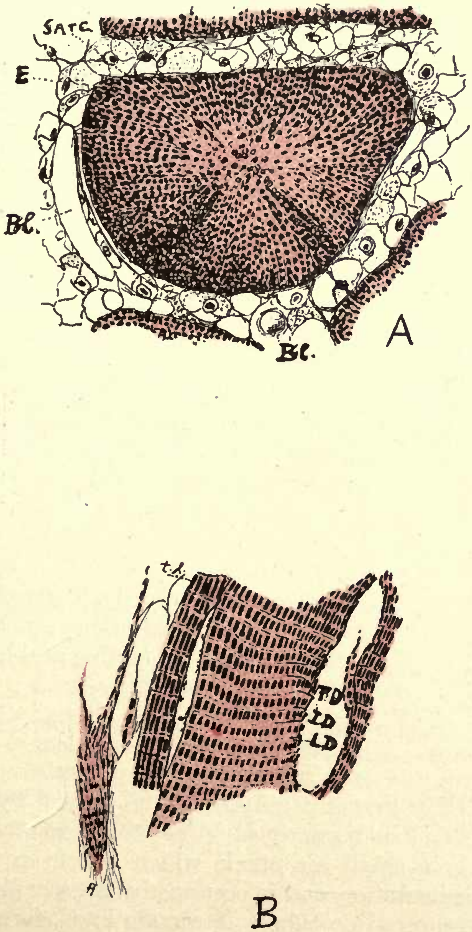


Fig. 19.—Striated muscle. (Slightly magnified.) *A*, cross section; *B*, longitudinal section; *Sarc.*, sarcolemma; *Bl*, blood vessels; *E*, endomysium; *TD*, transverse disc; *ID*, intermediate disc; *LD*, Lateral disc.

converted into ground glass at regular intervals. The dark bands are known as *transverse discs,* and the lighter ones as *lateral discs.* Each measures about 2μ in height, so that a segment of a length of 1 cm. contains close to 10,000 dark striæ.

The theories which have been put forth in order to establish a correlation between the structure and the function of this cell are many, but none may rightly be said to have given a correct interpretation of actual conditions. It is apparent that a contracting muscle cell shifts its substance in such a way that its length is considerably decreased in favor of its breadth. During this phase the dark bands become light, and the light bands dark. A rapid transfer of water from one disc into the other is said to be responsible for this change. What is true of each individual cell, is true of the muscle as a whole. On contraction, it increases its breadth at the expense of its length.

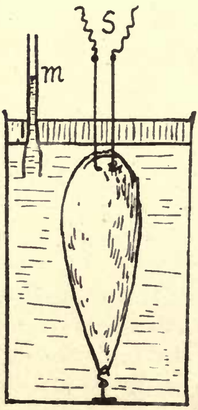


FIG. 20.—Schema to show that contracting muscle does not change its volume. *M,* meniscus of saline solution; *S,* electrodes through which muscle in receptacle is stimulated.

It should be clearly understood, however, that a muscle does not change its volume when contracting and hence, does not acquire material from without in order to bring this change about. Its contraction merely consists of a peculiar re-arrangement of its substance. This point may easily be proved by placing a muscle, such as the gastrocnemius of the frog, in a small receptacle which has been filled with boiled saline solution and is equipped with a capillary tube. The saline enters this tube to a certain level, forming here a meniscus. If the muscle is now made to contract, the latter remains perfectly stationary.

Cardiac Muscle Tissue.—The wall of the heart is composed of a lining or endocardium, a layer of muscle tissue or myocardium, and an enveloping membrane or epicardium. The

latter is reflected from the large blood vessels in the form of the pericardium, enclosing a very narrow space which is filled with a lymph-like fluid. Like in the other contractile tissues, the myocardium consists of a framework of connective tissue in which are embedded the individual rows of cardiac muscle cells. Inasmuch as the heart possesses the shape of a tube and inasmuch as the principal layer of this muscle is arranged circularly around the lumen of its cavity,

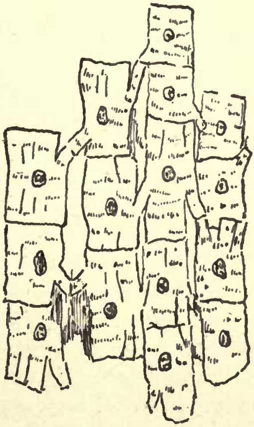


FIG. 21*A*.—Cardiac muscle.

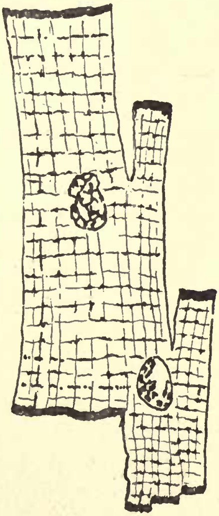


FIG. 21*B*.—Single cardiac cells. Magn. 1000.

the contraction of these cells must decrease its capacity, thereby placing the blood within under a higher pressure than before.

If we now place one of the fibers or rows of cardiac muscle cells under the high power of a microscope, it will be seen that each component cell possesses the shape of a short cylinder and presents a rather square outline. Its rounded nucleus occupies the central region of its cytoplasm. These cells are beset with blunt processes which are connected with similar projections from the cells in the adjoining

columns. This is of the greatest functional importance, because the wave of irritability causing this muscle to contract, is thereby enabled to skip from cell to cell throughout the cardiac musculature. Owing, therefore, to its net-like structure, even a slight stimulus is sufficient to incite a reaction in all of its components. Contrariwise, the cells of striated and smooth muscle possess a certain independency, because each element is invested by sarcolemma and intercellular material. A slight stimulus applied to a muscle of this kind involves only a limited number of contractile elements. For this reason, the amplitude of the reaction of striated and smooth muscle must bear a direct relationship to the strength of the stimulus, whereas cardiac muscle always reacts maximally under ordinary conditions of excitation. This constitutes the so-called all-or-none law of cardiac muscle. It implies that the contractions of this tissue are always large in amplitude irrespective of the strength of the stimulus, and that its reaction cannot be graded accordingly.

CHAPTER VI

THE MANNER OF CONTRACTION OF MUSCLE

Manner of Excitation.—Muscle tissue is in possession of a certain amount of contractile substance which may be activated at intervals by stimuli. Thus, the heart of a cold-blooded animal may be excised and kept beating in a dish for several weeks, provided it is immersed in a nutritive solution of suitable temperature. The same results may be obtained with the hearts of warm-blooded animals. Consequently, this organ must embrace all the prerequisites for its activity, and its connections with the central nervous system can only serve the purpose of adjusting its action to those of other structures. Likewise, we are able to excite rhythmic responses in excised striated and smooth muscle, provided we expose these tissues to the solutions of certain salts. Moreover, it is a matter of common experience that normal muscles may be activated by applying electrical or mechanical stimuli directly to the skin overlying them.

Under ordinary circumstances, however, both types of muscle tissue are under the control of special nerves and centers, and besides, striated muscle is under the influence of volition. The nerve cells composing these centers generate impulses which pursue a definite course outward to their respective muscles, causing them to contract. As far as those skeletal muscles are concerned which are employed in locomotion, it is known that their control is effected through a group of large, pyramidal nerve cells which are situated in the anterior central convolution of each cerebral hemisphere. In accordance with its function, this particular region of the brain is called the motor area. The muscles on the left side of the body are dominated by the cells in the right half of the cerebrum, and those on the right side by the cells in the left hemisphere. This peculiar innervation is brought about by

the fact that the nerve fibers emerging from one motor area, cross over to the other side of the body in the medulla and

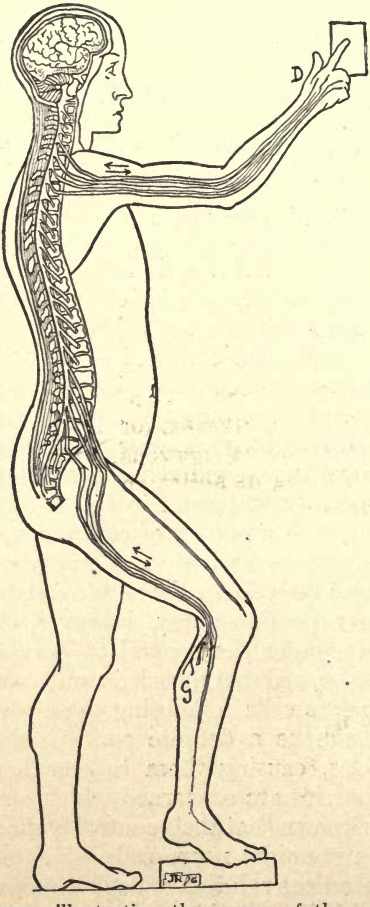


Fig. 22.—Diagram illustrating the course of the sensory and motor fibers between the brain and such parts as the fingers (*D*) and gastrocnemius muscle (*G*).

spinal cord. For this reason, an injury to one of these motor areas invariably causes the muscles on the opposite side to become paralyzed.

It may be said, therefore, that the skeletal muscles are activated under normal conditions in an *indirect* way in consequence of the influx of impulses generated in certain nerve cells. Whenever these impulses are unable to reach a muscle, the latter remains inactive. Such a condition may arise either in consequence of an injury to the center destroying its generating power, or as a result of a break in the conducting path, occasioned in many instances by nerve section. A muscle rendered inactive in this manner is said to be paralyzed. Because of this loss of stimulation it finally undergoes certain retrogressive changes which betray themselves in a diminution in its irritability, volume, and weight. The skeletal muscles may also be activated *directly* by the stimulation of the skin overlying them or by the excitation of their motor nerves.

Smooth muscle is also under the control of nerve centers, but these centers are not dominated by volition, and frequently lie in the organ itself or in its immediate vicinity. To be sure, these local stations are connected with the central nervous system by special nerve fibers, but these paths are present chiefly for the purpose of correlating the action of one organ with that of another.

Muscle Tonus.—When resting, a normal muscle is never fully relaxed, but is retained in a position of elastic tension, intermediate between complete relaxation and contraction. The condition of tonus, therefore, simulates an incomplete relaxation. Only a paralyzed muscle ceases to be in tonus and relaxes completely. This fact is important, because it places the muscle fibers in a position from which they can enter the state of contraction more quickly than from that of complete extension. Accordingly, this condition may be said to favor rapidity of action and to conserve muscular energy.

The cause of the tonicity of a muscle lies in an influx of impulses from those nerve cells which control its action. These impulses are discharged at the rate of ten in every second and do not evoke a visible reaction. They are, therefore, subminimal in their intensity, causing the muscle substance to retain a condition of functional alertness, ready at any

moment to respond to impulses of supra-threshold value. The aforesaid nerve cells in turn are forced to continue their activity by diverse sensory impulses. When the latter cease, the nerve cells become inactive and discontinue to generate those impulses upon which the tone of muscle depends.

Good posture depends upon the tonus of many associated groups of skeletal muscles. Thus we note that the paralysis or complete loss of tonus of a group of muscles causes the part moved by them to become flaccid and to assume a position out of the ordinary. Diminutions in the tonus of the skeletal muscles are frequently experienced in consequence of mental and bodily fatigue and in the course of many intoxications. Such organs as the stomach, intestine, and bladder undergo constant fluctuations in tonus. Hence, a stomach considerably enlarged by food need not be more forcibly distended than one practically empty, because its wall accommodates itself to the varying amount of contents by simply changing its tone. Accordingly, the wall of a highly distended organ need not exert a greater pressure upon the contents than the one of a partially filled organ.

It may rightly be concluded that a muscle out of tonus cannot react as well as one in tonus. This statement, however, should not be interpreted as signifying that an atonic muscle cannot be made to contract at all, because an absolute functional uselessness presupposes a severe disturbance in its metabolic condition. Thus even a paralyzed muscle may be stimulated directly with positive results until it is no longer able to acquire the necessary contractile material. Inasmuch as the nutritive state and power of contraction of a muscle depend upon its activity, we usually endeavor to retain a paralyzed muscle in an at least partial condition of usefulness by repeated massage and direct electrical stimulation. Meanwhile, possibly, the injury to the nerve center or to the conducting path may be remedied, so that the muscle may again come under the influence of normal impulses and regain its former tonus and contractile strength.

The Elasticity of Muscle Tissue.—It is a well-known fact that a fresh rubber band may be successively extended by

weights, the degree of its extension being each time proportional to the weight. Furthermore, provided the total load is not excessive, the rubber band will again recoil into its former state when the weights are removed. When left in the body, a normal muscle presents the same tendencies, *i.e.*, it resumes its previous shape and position when detentioned. An excised muscle, on the other hand, is imperfectly elastic, and does not fully recover its former degree of tension after it has been stretched by weights. No doubt, this procedure has led to a permanent displacement of

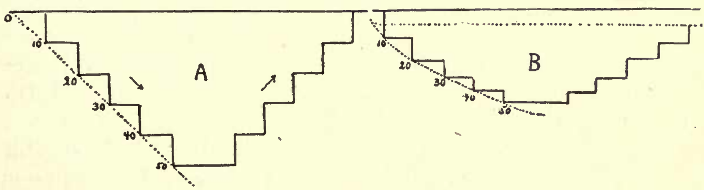


FIG. 23.—Extensibility and elasticity. *A*, rubber band and *B*, gastrocnemius muscle of frog successively loaded with 10 gram weights. The second curve shows a decreasing extension for equal increments, hence, the line joining the ends of the ordinates is curved.

its component cells. An excessive weight will finally rupture the muscle. The breaking point in the case of the excised gastrocnemius muscle of the frog lies near 1000 grams. Long before this point is reached, however, some of the strands of connective tissue are torn away from their connections with the muscle fibers. This is the most frequent cause of muscle strain and consequent stiffness. The pain felt in a muscle which has been injured in this way is severe in character, and may continue for some time, indicating the slow manner of repair of a lesion of this kind. The spraining and tearing of the tendons themselves usually leads to extravasations of serous fluid into the adjoining soft parts.

The Wave of Contraction.—A short and compact skeletal muscle usually receives its nerve supply at its upper pole, whereas a long muscle receives it about midway between its

two ends. From here the delicate fibrils are then distributed to the individual cells in its two poles. This arrangement possesses an important practical bearing, because if the different portions of a striated muscle actually contracted at recognizable intervals, the best mechanical results could not be obtained. Very slight differences in their contraction, however, are frequently present, and may be clearly demonstrated by means of sensitive measuring appliances. Experimentally, they may readily be produced by the excitation of a long muscle, such as the sartorius. When stimulated at one of its poles, a wave of contraction will arise in this region which then travels towards its other end, progressively involving its consecutive segments. Thus, if two levers are placed horizontally upon this muscle at an appreciable distance from one another, the lever nearest the seat of the excitation will be moved first.

Very conspicuous waves of contraction are discernible in smooth muscle tissue. Such organs as the stomach, intestine, ureter, or bladder show characteristic waves of peristalsis which slowly progress from one zone to another. A similar effect is noticeable in the heart, and especially in that of the lower forms, because the contraction of this organ is initiated at its venous entrance, whence it travels towards its apical portion. This statement implies that its vestibular portion completes its contraction before that of the auricles actually begins. Likewise, the contraction of the auricles is fully developed before that of the ventricles actually sets in. It need not be emphasized that this peristaltic manner of contraction is absolutely essential for the orderly flow of the blood through the different chambers of this organ.

The Bones as an Aid to Muscular Power.—It has been stated above that the skeletal muscles may be arranged in two groups, embodying, on the one hand, those which use the bones as levers to increase their power, and, on the other, those which employ them merely as simple points of attachment. It will be remembered that a lever is a rigid bar, one part of which is fixed while the other is freely movable. It presents a part to which the power is applied to overcome the obstacle (*P*), a part of support or fulcrum (*F*),

and a point of resistance acting against the weight or obstacle (*W*). In accordance with the relative positions of these points, the mechanician recognizes three systems of levers: namely,

(*a*) The fulcrum is situated between the power and the weight. As an example of this kind might be mentioned the rocking of the head upon the atlas as fulcrum. The

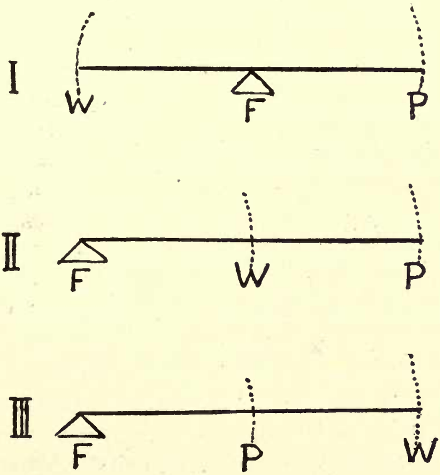


FIG. 24.—Different systems of levers. *F*, fulcrum; *P*, power; *W*, weight.

muscles at the back of the neck then form the power, while the face represents the weight. This system may also be imitated by raising the foot and tapping the floor with the toes. In this case, the fulcrum lies at the ankle-joint, and the weight at the toes. The gastrocnemius muscle forms the power.

(*b*) The fulcrum is placed at one end, and the weight between it and the power. As an example illustrating this system might be mentioned the raising of the body upon the toes as during the first stage of stepping forward. The toes represent the fulcrum, while the power is furnished by the gastrocnemius muscle. The weight is applied at the ankle-joint.

(*c*) The fulcrum lies at one end and the power between it and the weight. In illustration of this arrangement might be mentioned the flexion of the forearm upon the arm. The fulcrum lies at the elbow-joint, and the weight at the hands, whereas the power is furnished by the biceps muscle. The tendon of the latter is inserted upon the radius.

Usually the pull of a muscle is exerted in a straight line to its axis, joining its points of attachment and insertion. Thus, the superior rectus of the eyeball moves the cornea upward, while the inferior rectus rolls it downward. Some muscles, however, do not show this arrangement, and give rise to a movement the reverse of what might be expected. For example, the superior oblique of the eyeball causes the cornea to move downward, because its tendon passes across a pulley-like structure before it is inserted upon the eye. Another peculiar arrangement is shown by the digastric muscle. As the name indicates, this muscle consists of two masses which are joined by a tendinous part, the latter being fastened to the hyoid bone by a pulley-like structure. Inasmuch as this muscle extends from the base of the skull to the anterior margin of the lower jaw, its contraction must aid in separating the lips and opening the mouth.

Different Types of Movements Employed in Locomotion.—The skeletal muscles of our body are usually arranged in such a way that their actions oppose one another. This point may best be illustrated by referring to the movements of the forearm in consequence of the contraction of the biceps and triceps muscles. The former is situated upon the ventral surface of the humerus, while the latter is placed upon its dorsal surface. When the biceps contracts the forearm is moved upward. This constitutes its flexion upon the arm. If the triceps is now activated, the forearm is again forced downward. This represents its movement of extension. Clearly, therefore, flexion and extension are antagonistic movements which are made possible by the activation of only one of these muscles. While one is contracted, the action of the other is inhibited. As far as the human body is concerned, flexion is usually accomplished in a forward direction. An exception to this rule is formed by the legs

which are flexed backwards. Besides flexion and extension, we recognize the movements of abduction and adduction, and rotation and circumduction.

(*a*) *Flexion* and *Extension.*—When the point of insertion of a muscle is brought closer to its point of attachment, the distant part of the limb is bent upon the central one. The straightening out of the limb constitutes the movement of extension. The flexion and extension of the forearm upon the arm comes to our minds first when seeking to illustrate this movement.

(*b*) *Abduction* and *Adduction.*—When a part is moved away from the medium line of the body, it is abducted, and when drawn toward it, adducted. As an example of this type of movement might be mentioned the abduction and adduction of the thigh.

(*c*) *Rotation* and *Circumduction.*—A part is rotated when it is made to turn upon its axis. For obvious reasons, perfect rotations, as exemplified by the wheels of a wagon, are not possible. The acrobat who is able to suspend himself from a horizontal bar with his arms and to rotate his body in the glenoid cavity more than once, must have acquired an extreme movability of the head of the humerus in its capsule, so that he is able to dislocate it at will. The supination and pronation of the hand belong in this group of movements. Circumduction is accomplished by describing a conical surface by rotation around an imaginary axis.

CHAPTER VII

ANALYSIS OF MUSCULAR CONTRACTION

The Simple Twitch.—When a skeletal muscle contracts its point of insertion is brought closer to its point of attachment. We have seen that this change is brought about by the shortening of the entire muscle and hence, also of its individual cells. In the normal muscle this movement may be

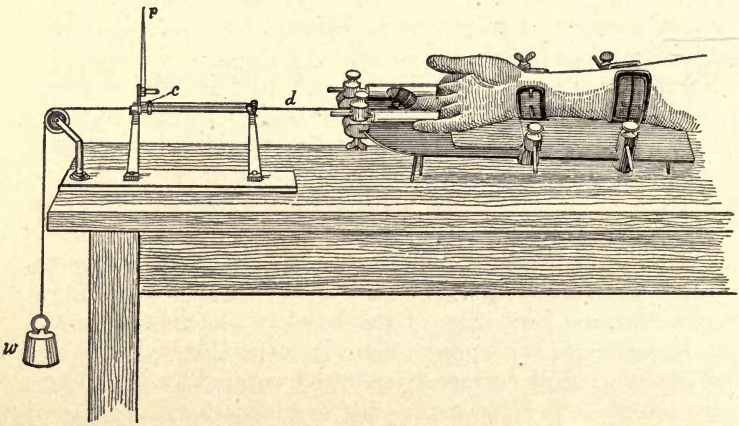


FIG. 25.—Mosso's ergograph. *c*, is the carriage moving to and fro on runners by means of the cord *d*, which passes from the carriage to a holder attached to the last two phalanges of the middle finger (the adjoining fingers are held in place by clamps); *p*, the writing point of the carriage, *c*, which makes the record of its movements on the kymograph; *w*, the weight to be lifted. (*Howell.*)

conveniently studied by means of the apparatus shown in Fig. 25. It is usually designated as an ergograph, and consists of a support for the forearm and a weight which is connected with one of the fingers by means of a sling and cord. The weight is equipped with a writing lever which is

permitted to rest against the smoked paper of the drum of a kymograph. When the finger is alternately flexed and extended, the movements of this part are registered by the weight upon the paper. The phase of contraction is indicated by the upstroke, and the period of relaxation by the

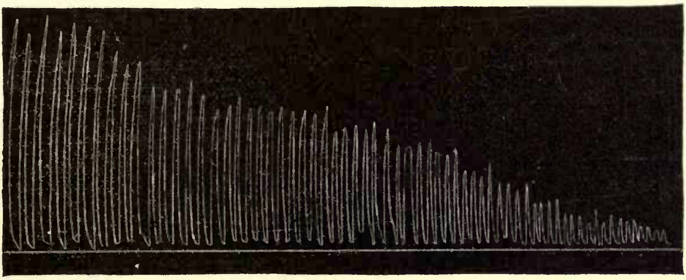


Fig. 26.—Normal fatigue curve of the flexor of the index finger. Weight, 3 kg.; contractions repeated every second.

downstroke of the writing lever. Obviously, these phases appear upon the paper of a stationary drum in the form of single vertical lines. When, however, the drum of the kymograph is made to revolve, the upstroke and downstroke of the curve become widely separated from one another, and

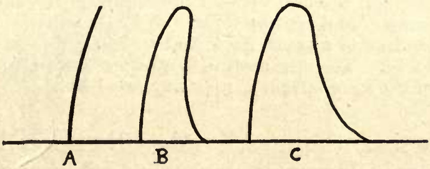


Fig. 27.—Muscle curves recorded with different speeds of the drum of the kymograph.

the more so, the greater the speed of the drum. Curves of this kind are represented in Fig. 27.

The minute character of a muscular contraction may also be studied by fastening an excised muscle in a stand in such a way that its tendon remains free to act against a writing lever adjusted upon the smoked paper of a kymograph.

The muscle usually employed for this purpose is the gastrocnemius of a recently killed frog. Its upper pole is securely fixed in a clamp, while its tendon is connected with the writing lever distally to its center of rotation. A slight weight is then attached to the lever directly underneath the tendon.

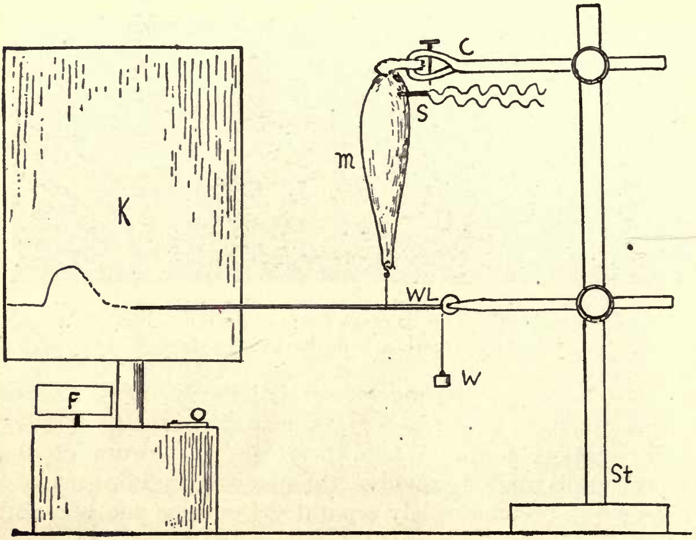


Fig. 28.—A method used to register muscular contraction. *St,* stand for holding of clamp *C* and writing lever. *WL,* the muscle *M* is attached to the lever by means of a small hook and string. The lever is counterpoised by weight *W*. The stimulation is effected through the electrodes, *S*. The speed of the kymograph *K* may be varied by fan *F*.

When contracting, the muscle raises the lever to a certain height, but again lowers it during its subsequent phase of relaxation. The greater the speed of the drum, the more widely will these two limbs of the curve be separated from one another.

We have previously noted that a muscle in situ is stimulated under ordinary circumstances in an *indirect* manner by impulses conveyed to it through its motor nerve. But it is also possible to activate it in a *direct* way by applying artificial stimuli to the skin overlying it. An excised muscle,

on the other hand, can only be made to contract by artificial stimuli, and these stimuli may be passed into it by bringing the wires from the battery in direct contact with its substance or that of its nerve. Electrical stimuli are employed because they are more easily produced and applied than the others. The time which the muscle requires for its contrac-

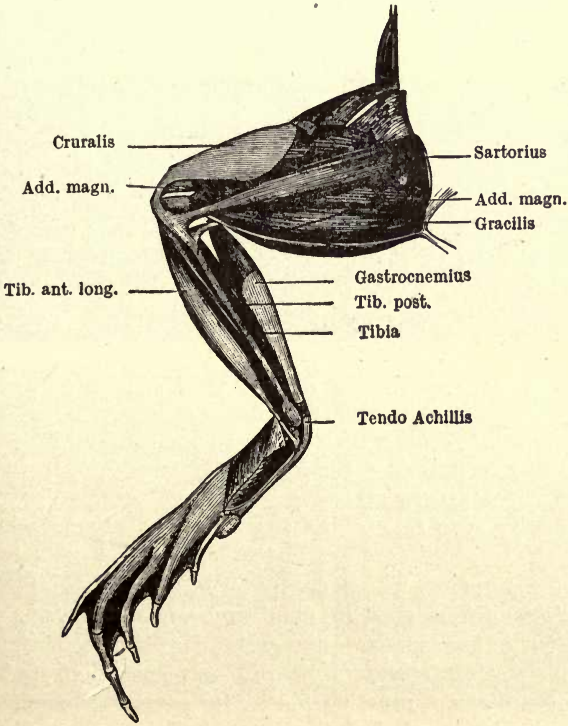


FIG. 29.—The muscles of the hind leg of frog. (*Ecker.*)

tion, may be ascertained by permitting a tuning fork to register its vibrations below the line of the muscle lever. Lastly, it is advisable to record the moment when the electrical shock is sent into the muscle or its nerve by means of an electro-magnetic signal inserted in the battery circuit.

When a muscle is made to register its contraction under

these circumstances, it yields a curve such as is represented in Fig. 30. This curve consists of two principal phases, representing the periods of shortening (*C*) and relaxation (*R*) of the muscle. If a comparison is now made between the beginning of the phase of contraction and the moment of stimulation (*M*), it will be noted that the muscle does not react precisely when stimulated but a little later. The time elapsing between the moment of stimulation and the onset of

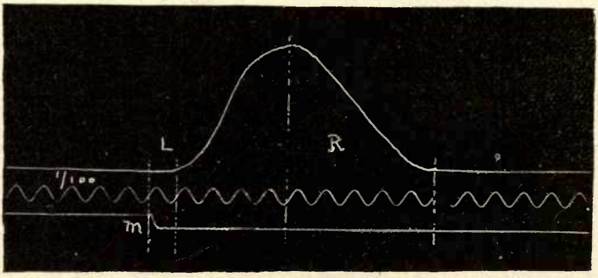


Fig. 30.—A muscle twitch. ***M*, make shock recorded by magnetic signal connected with primary circuit. Time in 1/100 sec.; *L*, latent period; *C*, period of contraction; *R*, period of relaxation.**

the reaction, constitutes the latent period (*L*). During this phase diverse processes are promulgated in its substance, which finally give rise to the shortening of the muscle as a whole.

The time during which a muscle is able to complete its contraction, differs with its condition at the time of experimentation. If we confine ourselves at this time to the gastrocnemius muscle of the frog, it will be found that its latent period usually consumes 0.01 sec., its period of contraction 0.04 sec., and its period of relaxation 0.05 sec. A rapid contraction of this kind following a single stimulus, is known as a twitch. It should be remembered, however, that this time of 0.1 sec. is by no means the shortest recorded in any muscle, because the wing-muscles of the insects contract two and three hundred times in a second.

Summation of Contraction.—If a second stimulus is applied to the muscle shortly after the beginning of its

period of relaxation, a second contraction will be obtained which is higher than the first. In the same manner a third contraction may be mounted upon the second, and so on,

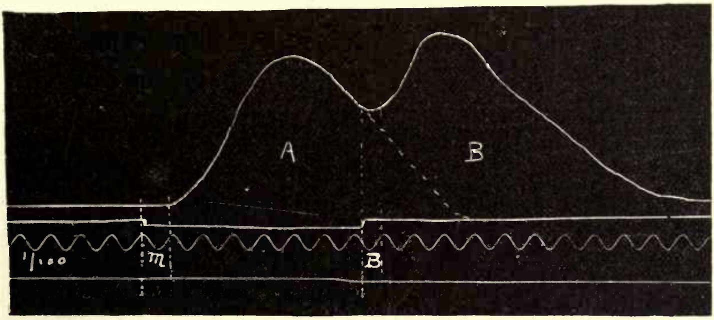


FIG. 31.—Summation of contractions. *M* and *B*, make and break shocks indicated by an electro-magnetic signal. Time in 1/100 sec. As the break contraction occurs during the period of relaxation of the make contraction, it is added to the first.

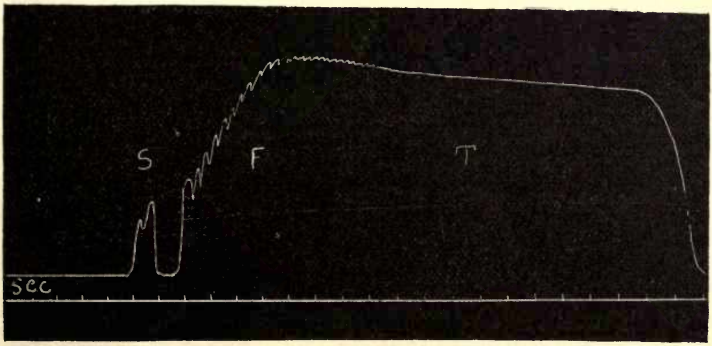


FIG. 32.—Fusion and tetanus. *S*, summation; *F*, fusion; *T*, tetanus. Time in seconds. The individual make and break shocks are repeated so quickly that a continuous contraction is obtained.

until the individual contractions become partially fused into an *incomplete tetanus*.

Tetanic Contraction.—If the individual electrical shocks are repeated at a still more rapid rate, the muscle cannot

relax at all and remains in a state of maximal contraction. The incomplete tetanus is then changed into a complete tetanus. Ordinarily about 20 to 50 stimuli in a second are required to tetanize the gastrocnemius of the frog. It is true, however, that the contractile material of this muscle is rapidly used up during this prolonged form of contraction,

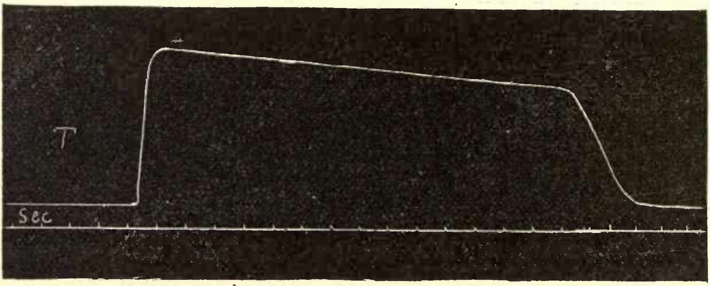


FIG. 33.—Tetanic contraction. Recorded by means of Neef's automatic interrupter. Time in seconds. The decline of the curve is an indication of fatigue.

and that this partial depletion of its energy store finally induces a certain degree of *fatigue* which is indicated in the curve by a slow decrease in its height. When completely fatigued, the muscle returns into its position of relaxation in spite of the continuance of the excitation.

Repeated determinations of the contraction-time of human muscles have shown that they do not respond so swiftly as the muscles of the cold-blooded animals. Even such a brief muscular response as is required to close the eyelids is tetanic in its nature.[1] The same statement may be made regarding the trained movements of the fingers of a pianist or typist. A speed of ten in a second is rarely attained. Accordingly, it is believed that the contractions of our skeletal muscles are the result of a series of nervous stimuli and not of a solitary one. Thus, it will be seen that if a certain muscle is

[1] In medical literature the name tetanus refers to lock-jaw. In this disease the muscles, and especially those attached to the lower jaw, become firmly contracted.

to be contracted, the corresponding motor nerve cells send out rhythmic discharges which do not cease flowing until the contraction is to be discontinued. These cells, therefore, may be compared to batteries discharging through a vibrator.

The closest approach to a simple twitch is presented by cardiac muscle. Smooth muscle tissue responds very sluggishly. All of its phases are very much prolonged, so that the latent period may occupy several seconds instead of a few hundredths of a second. The total length of its contraction depends, of course, upon the intensity of the stimulus, but assuming that such a preparation as the cat's bladder has been subjected to a tetanizing current of moderate strength and duration, it may take 3 to 6 minutes before its muscle cells again assume their original length.

The Factors Modifying the Height of Contraction.—It is a matter of common experience that the amplitude of the

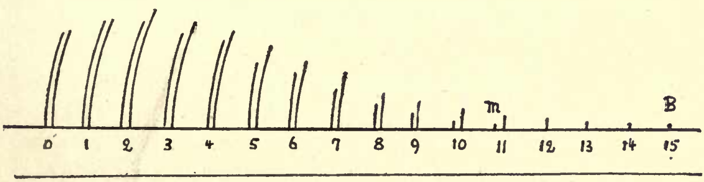


FIG. 34.—Successive make and break contractions. The strength of the current is gradually diminished by more widely separating the secondary from the primary coil. The figures indicate this separation in centimeters of distance. *M*, threshold of make; *B*, threshold of break.

contractions of heart muscle remains practically the same, whereas that of the contractions of striated and smooth muscle may be varied considerably. The principal factor responsible for this change is the *strength of the stimulus*. If an excised striated muscle is stimulated successively with single shocks of decreasing intensity, a curve is obtained such as is represented in Fig. 34. This proves that the amplitude of reaction decreases steadily with the stimulus, although it is noticeable that supramaximal stimuli yield smaller responses than those of maximal value. It seems that a mild stimulus affects only a limited number of cells,

whereas a strong one activates a much larger number. This difference is not exhibited by cardiac muscle, because its cells are joined by short processes which permit the wave of excitation to spread rapidly from fiber to fiber. For this reason, heart muscle always reacts maximally, a fact which is commonly expressed by saying that this tissue follows the all-or-none law of contraction.

It may be stated in a general way that a lasting stimulus is a more efficient exciting agent than a brief one, but this relationship holds true only as long as its *duration* is not unduly prolonged. In the latter event, fatigue rapidly diminishes the amplitude of the contractions. As might be expected, *increasing weights* gradually reduce the height of muscular contractions. It is evident, however, that a slight load exerts a favorable influence, because it augments the elastic tension of the contractile elements (Fig. 35).

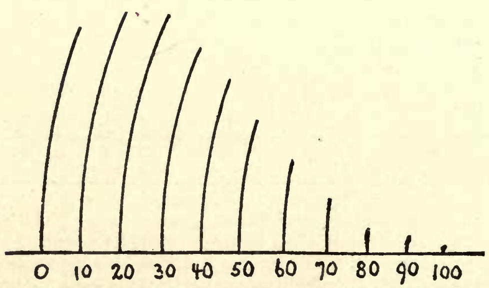


Fig. 35.—Influence of load. This muscle has been successively loaded with 10 gram weights.

The *character* of the *muscle substance* is another important factor, because upon it are based the power and rapidity of the reaction of the muscle. For example, since striated muscle contains a larger amount of water and smaller amount of undifferentiated sarcoplasm than smooth muscle, it is able to respond more swiftly than the latter. In this connection attention is also called to the fact that striated muscle is frequently made up of fibers of different quality, its "pale" constituents reacting more rapidly than its "dark" ones.

Warmth increases the amplitude of the contractions,

whereas *cold* decreases it. This may easily be proved by placing a gastrocnemius muscle in a compartment, the temperature of which may be changed at will. Fig. 36 represents

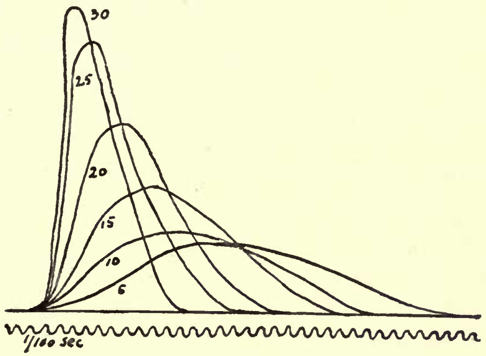


FIG. 36.—Effect of changes in the temperature on muscular contraction. The temperature was raised 5° each time.

a series of tracings taken at differences of 5° C. It will be seen that those recorded at low temperatures are very sluggish, while those registered at about 30° C. are very rapid. It is also to be remembered that the muscles of the frog begin to lose their irritability at about 37° C., and finally pass into the state of *heat-rigor* or *rigor caloris* (42° C.). When in this condition the muscle possesses on opaque appearance and is maximally shortened. It cannot be made to contract again. The optimum temperature for the muscles of warm-blooded animals is 37° C.

Certain *chemicals* affect the irritability and contractility of striated muscle in a most peculiar manner. Veratrin greatly prolongs its phase of relaxation. Potassium salts act as depressants, whereas sodium and calcium salts possess an excitatory action. A solution of 0.7 per cent. sodium chlorid is employed to keep the muscle in the best possible condition, because it is isotonic to its substance. Common stimulants of cardiac muscle are caffein and strychnin. Adrenalin diminishes muscular fatigue, owing to its stimulating action upon the circulation.

CHAPTER VIII

THE CHEMISTRY OF MUSCLE

Fatigue of Muscle.—If an excised muscle is stimulated a great many times, the height of the successive contractions gradually decreases, until the writing lever remains finally in the horizontal position. The length of the individual curves, however, is materially increased. This gradual decline in the power of the muscle to respond to stimuli is known as fatigue. It is to be remembered, however, that a muscle on repeated contraction shows first a slight augmentation before its reactions are actually diminished. This brief initial gain in height corresponds to the process of "warming up" of the normal skeletal muscles of the higher animals. It is also of interest to note that a fresh gastrocnemius muscle is able to contract more than one thousand times before it becomes functionally useless. Moreover, this condition of fatigue is permanent, *i.e.*, the muscle cannot be made to contract again even after a long period of rest. This result suggests that its store of contractile material has been completely exhausted and, naturally, an excised muscle possesses no means of rebuilding the substances which it has lost during its preceding reactions.

Since a normal muscle is in a very favorable position to replenish its contractile material, it cannot be so thoroughly fatigued as an excised one. But, there is another factor which plays an important part in the production of this phenomenon, and that is the accumulation of the waste products formed in the course of muscular metabolism. An engine may stop on account of a shortage of fuel, but also because its exhaust pipes have become clogged with the products of combustion. A normal muscle is constantly flushed out with blood containing nutritive substances and oxygen. In the presence of this gas the waste products

formed in the course of muscular contraction, are quickly oxidized and excreted. Since an excised muscle is not in possession of an unlimited supply of oxygen, it cannot rid itself of these injurious substances. Much of this elimination is accomplished during bodily rest, a state diametrically opposed to the state of work, and, naturally, the most complete repair is had during sleep when the muscles are fully relaxed and no demand is made upon their store of energy.

The Chemistry of Muscle.—The importance of the muscles in animal economy is clearly betrayed by the fact that about 42 per cent. of our weight is due to this tissue. In further illustration of this point, it might be mentioned that about 50 per cent. of the total metabolism of a resting person is apportioned to this tissue, and that a person in moderate activity may attain a muscular metabolism of as much as 75 per cent. of the total. These values immediately bring up the question regarding the character of the substances in normal muscle which may be held responsible for this surprisingly large production of energy. While the succeeding table illustrating the composition of muscle tissue may be of service in answering this query, this subject-matter cannot be fully understood until the contents of the subsequent paragraphs have been noted.

Water	74.0 per cent.
Solids	26.0 per cent.
Proteins	18.0 per cent.
Collagen	2.0 per cent.
Fat	2.0 per cent.
Glycogen less than	1.0 per cent.
Creatin	0.3 per cent.
Other organic substances	
Inorganic substances	3.0 per cent.

The Chemistry of Contracting Muscle.—The metabolic changes in muscle on contraction are characterized by a constancy of the catabolism of the proteins and an increase in the catabolism of the carbohydrates. Accordingly, muscular work is not followed by a greater nitrogen output, but by a disappearance of glycogen, a substance closely

allied to ordinary starch. This change is associated with a production of lactic acid and elimination of much larger amounts of carbon dioxid. It must be evident, therefore, that the energy liberated by muscle is chiefly derived from the carbohydrates of the food.

The production of carbon dioxid is indicated by the fact that the expired air contains larger amounts of this gas. To be sure, the oxygen intake is also augmented, but the absorption of this gas remains below the output of carbon dioxid. It is a matter of common experience that muscular exercise is always accompanied by a greater respiratory activity.

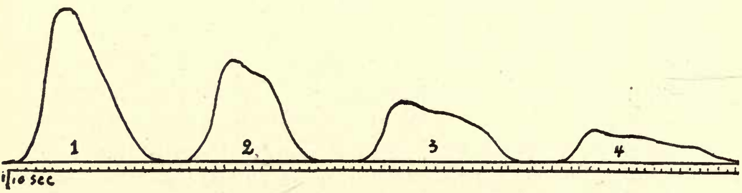


FIG. 37.—Fatigue of muscle. A gastrocnemius muscle of the frog stimulated successively 150 times. The 1st, 50th, 100th, and 150th contractions are recorded.

Resting muscle is neutral or faintly alkaline in its reaction, whereas active muscle is distinctly acid. This acidity finds its origin in an accumulation of sarcolactic acid. Consequently, much larger amounts of this acid must be present in an excised muscle than in one able to obtain fresh oxygen, because in the presence of this gas this waste product is quickly reduced. This diminution in the store of glycogen may be proved in a quantitative way. Thus, it has been found that frog's muscle loses from 24 to 50 per cent. of its glycogen when tetanized, while a resting muscle contains considerable amounts of this substance.

The Fatigue Substances.—We have previously noted that the excessive stimulation of a muscle causes it to lose its irritability and contractility. Even a very strong stimulus is then no longer able to activate it. This functional exhaustion has been referred to two causes: namely, an inadequate acquisition of energy yielding material and an accumulation

of certain waste products. The latter are frequently designated as fatigue substances. The fact that such bodies are actually liberated and enter the circulation, has been proved by permitting the blood of a fatigued animal to flow into the circulatory channels of a perfectly normal one. The latter then exhibited the phenomena of fatigue as if it itself had been subjected to excessive muscular exercise.

The principal fatigue substance is an acid which is similar in its constitution to the acid formed in the process of souring milk. It is usually called sarcolactic acid to distinguish it from the lactic acid of milk. Other fatigue substances are carbon dioxid and acid potassium phosphate. It has also been noted that certain toxic bodies are produced, but this point has not been definitely settled as yet. It is obvious that these so-called fatigue substances are liberated in the course of muscular metabolism, and are able to evoke this characteristic action because they are only partially oxidized. The symptoms resulting in consequence of the accumulation of these metabolites are local as well as general in their character, *i.e.*, besides the localized feeling of discomfort and pain, one also experiences a general lassitude of body and mind. But while muscular fatigue usually induces mental fatigue, it may also happen that these events are reversed. Thus, we well know that mental fatigue is usually associated with a lassitude of the entire body. The manner in which this reaction is brought about is not quite clear, although it is entirely probable that the nervous tissue generates a set of catabolic products very similar to those of muscle tissue. It may be concluded, therefore, that this relationship between the muscles and the central nervous system is dependent not only upon nervous reflexes but also upon definite chemical substances.

The excessive exercise of the muscles when not accustomed to it, frequently gives rise to a complex of symptoms, the most annoying of which is a painful stiffness of the musculature. In addition, one may experience a general discomfort, inability to work, lassitude, and a slight febrile reaction. Pertaining to the cause of the local symptoms, it is commonly stated that they find their origin in the excessive displace-

ment of the muscle fibers and the "drying up" of the intercellular material. Very similar results often follow the violent manipulation of the muscles with the fingers, as during massage. The general symptoms are referable to the toxic action produced by the fatigue substances.

The Chemistry of Rigor Mortis.—It is a well known fact that the muscles of the mammals become perfectly rigid very shortly after the blood has ceased to circulate. This condition which is known as death-rigor, or rigor mortis, lasts for a certain period of time and then disappears. Dissolution setting in the muscles resume their soft consistency, but cannot be made to contract again. Inasmuch as the skeletal muscles are frequently arranged in an antagonistic manner, their simultaneous rigidity must give rise to an inflexibility of the part normally moved by them. For this reason, the arms and legs cannot be bent at this time unless the tendons of their muscles are torn.

The time required for the development of rigor mortis varies considerably. Most generally, it appears in the course of a few hours, but sometimes only after about twenty-four hours. In cases of extensive laceration of the central nervous system, it has been known to set in almost instantaneously. The duration of death rigor also varies materially. Sometimes it terminates within a few hours, and sometimes only after several days. Several factors are at work to cause this divergency; for example, the temperature, the condition of the body at the time of death, the age of the individual, and the type of the lesion terminating life.

It is believed that rigor mortis is due to the coagulation of the protein material of muscle. The soluble proteins are temporarily converted into their insoluble form under the influence of lactic acid. When the acidity has again been destroyed by the slow oxidation of the lactic acid, the reverse chemical change permits the muscles to acquire their former soft texture.

The Production of Energy in Muscle.—When a muscle contracts, its stored energy is liberated to yield certain mechanical changes. But before this evolution of mechanical energy can be repeated, the muscle must oxidize a certain

amount of material and store it in some form ready for the next contraction. During this process of acquiring stored energy, it liberates heat and a small amount of electricity. It appears, therefore, that these forms of energy are not evolved simultaneously, but successively, and that the oxidations really succeed the actual contractions, their purpose being to reform the material lost during the preceding period of activity. In building a pier the individual posts are driven into the ground by letting a weight drop upon them. The potential or resting energy contained in the weight suspended high up between its guides, is converted into kinetic energy by its fall. This phase corresponds to the period of contraction of the muscle and its resultant liberation of mechanical energy. But, before the weight can again produce an impact, it must first be raised to its former height by steam power. Quite similarly, a muscle must first be placed in a proper condition for its succeeding mechanical action by oxidations. During this reaction heat and electricity are evolved.

As a rule, about 33 per cent. of the total energy of muscle is liberated as mechanical energy, but this percentage may be raised somewhat by placing the muscle under the best possible conditions for work. In order that muscle tissue may actually furnish work, it must be weighted and raise this weight to a certain height. Clearly, if it contracts without a load, it cannot change external conditions and hence, cannot yield any work. Likewise, it cannot furnish work if loaded with a weight so heavy that it cannot lift it. In this instance, most of the energy liberated by it is converted into heat.

Under ordinary circumstances, we ascertain the work performed by a muscle by multiplying the weight by the height to which it has been lifted. The product W is expressed in milligram-meters. Thus, if 25 grams have been raised to a height of 10 millimeters, as determined by the height of the curve recorded upon the paper of the kymograph, the muscle has accomplished 250 gram-millimeters of work. In this calculation, however, an allowance should be made for the magnification of the writing lever, as follows: $L:H::l:h$.

In this formula L indicates the total length of the lever, l the length of its short lever from the axis to the point of attachment of the muscle, H the height of the contraction, and h the actual height to which the load has been lifted.

The heat produced by muscle may be ascertained by means of different appliances which, however, cannot be described in detail at this time. It is of importance to remember that the muscles are the principal source of the body-heat, because they form 40 per cent. of the weight of our body and possess a very intense metabolism. It is a matter of common experience that our body-temperature may be raised several degrees by simply indulging in moderate muscular exercise for a relatively brief period of time, but the heat so generated is again dissipated within a few minutes. Consequently, a lasting effect cannot be produced in this way. This fact merely reveals the paramount importance of the muscles as heat-producing organs. Entirely in agreement with it, a person who is about to perform muscular work, selects a cool room and wears relatively thin clothing, so as to be able to transfer his heat more rapidly to the air. At the end of the exercise, however, he should protect himself well against an excessive loss of heat and its consequences, for as his skin is moistened with perspiration, he is in a relatively unfavorable position to counteract heat radiation. Woolens are well adapted to conserve the body-heat, because they are hygroscopic and do not allow the sweat to evaporate too rapidly.

An active muscle also presents certain changes in its electrical potential. Since the contraction traverses its substance in the form of a wave, one pole of it must be active while the other is resting. By the use of very sensitive electrical measuring devices, it has been ascertained that the resting portion of a contracting muscle is electro-positive to its active portion. This subject-matter will again be considered later on in connection with the electrical variations occurring in the beating heart. This organ exhibits very characteristic differences in its electrical potential, which may be accurately registered by means of an instrument, known as the string-galvanometer.

CHAPTER IX

THE NERVE IMPULSE AND REFLEX ACTION

The Structure of Nervous Tissue.—The tissue composing the nervous system, consists of a supporting framework and numerous generating and conductile elements or neurones. The reticular tissue appears in the form of investments and membraneous partitions of connective tissue, enclosing a network of spider-like cells which are known as neuroglia or glia cells. In the spaces formed by the latter are situated the neurones, the building stones of the nervous system.

Every neurone or nerve-cell is composed of a cell-body and several well differentiated processes. The *cell-body* may be round, oval, stellate, pyramidal, or pear-shaped, and possesses a diameter varying between 10 and 150μ. Its cytoplasm is faint granular in appearance, and contains a very conspicuous nucleus and nucleolus, as well as dark irregular bodies which are known as Nissl's granules. The processes with which the cell-body is equipped, are designated as *dendrites* and *axones*. This differentiation is made chiefly upon histological grounds, because the former appear as short, irregular, many-branched offshoots which remain in the immediate vicinity of the cell-body, whereas the latter are long, and pursue a rather straight course. They give off very few branches which are known as collaterals. Moreover, while a nerve-cell may be in possession of many dendrites, it usually exhibits only one axone. The former serve as points of entrance for the nerve impulses coming from different neighboring cells, while the latter constitutes its distributing channel.

Naturally, these processes extend for different distances through the nervous system, but if we select for purposes of illustration the path which connects a muscle of the foot with its motor cells in the cerebrum, we will find that

these extreme points of the body are brought into functional relation by only two neurones. The cell-body of the first lies in the motor area of the cerebrum, while its axone passes outward through the spinal cord as far as the lumbar region. At this level, it breaks up into its terminals which in turn are connected by contact with the dendrites of the cell-body of

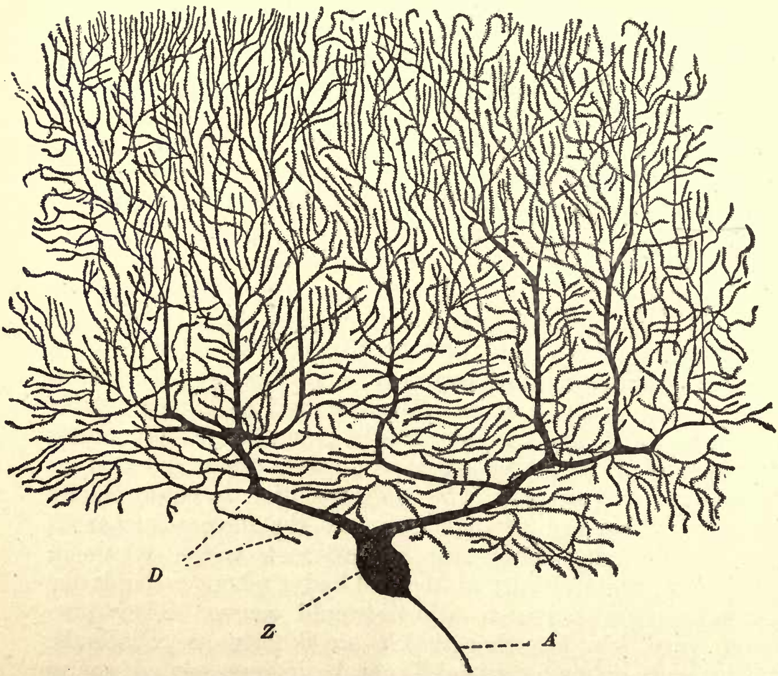


FIG. 38.—Purkinje cell from human cerebellum. Golgi's method of staining. (*Stöhr.*)

the second neurone. The axone of the latter then follows the highway of the sciatic nerve to the foot. Accordingly, each neurone must measure close to one meter in length.

In the case now under consideration, the cell-body is placed at one end of the neurone. This arrangement is always present in neurones which convey the nerve impulse in a direction from center to periphery. They are known as

motor or *efferent* neurones. Those nerve-cells, on the other hand, which conduct impulses from the periphery to the center, display their cell-bodies at some distance from their terminals. They are known as *sensory* or *afferent* neurones (Fig. 39).

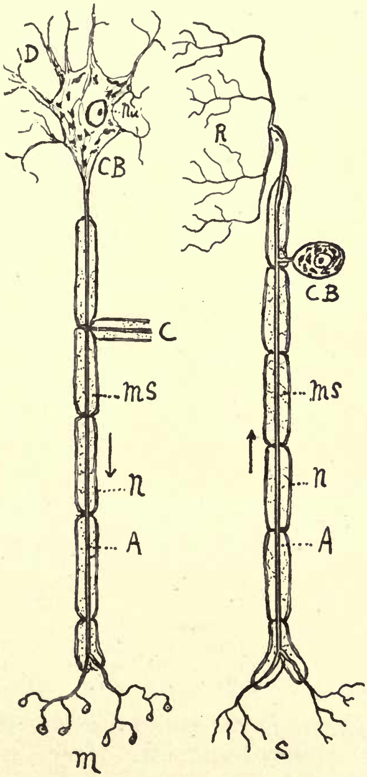


FIG. 39.—*M*, motor neurone; *S*, sensory neurone; *M*, motor end-organ; *S*, sensory end-organ; *A*, axis cylinder; *MS*, myelin sheath; *N*, neurilemma; *C*, collateral; *CB*, cell-body; *D*, dendrites; *Nu*, nucleus and nucleolus; *R*, sensory terminals.

Most generally, these sensory and motor neurones are joined in such a way that the terminal fibers of the former come to lie in close contact with the dendrites of the latter.

Such a point of union between neighboring neurones is termed a *synapse*. This adjustment permits the sensory or afferent impulse to activate the adjoining motor or efferent neurone. It is to be remembered, however, that the sensory impulse does not actually pass through the synapse and

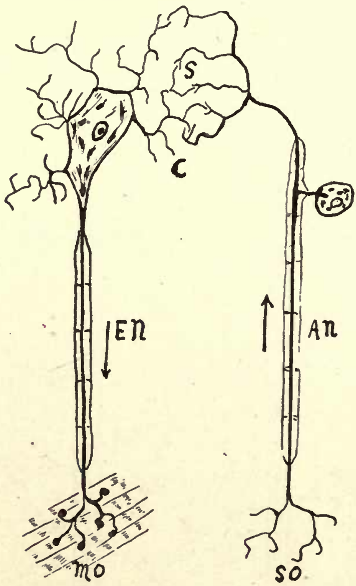


FIG. 40.—Reflex circuit. *SO*, sensory end-organ, receptor; *MO*, motor end-organ, effector; *AN*, afferent neurone; *EN*, efferent neurone; *C*, center; *S*, synapse.

continue through the motor neurone as an efferent impulse, but ends in the sensory terminals. Hence, the dendrites of the next motor neurone[1] are activated solely by contact

[1] The term motor refers more particularly to those efferent neurones which induce movement, *i.e.*, to musculo-motor fibers and nerves. Certain efferent nerves, however, evoke secretion, in which case they are designated as secreto-motor nerves. They may also control the discharge of electricity from special organs, as in the electrical fish, or give rise to an erection of the hairs, or a change in the caliber of the blood vessels. The terms of electro-motor, pilo-motor, and vaso-motor are then employed to characterize their function.

chemical? Acetylcholine!

and in a purely physical manner. The sensory impulse, therefore, is distinct from the motor impulse.

The structural arrangement in the synapse may be illustrated by placing the fingers of the left hand in the form of a basket around the index finger of the right hand. The latter then occupies the position of the terminal of the sensory neurone, and the former those of the receiving dendrites of the motor neurone. By separating these filaments of the synapse more widely from one another, a break may eventually be established between them, so that they can no longer give rise to the aforesaid transfer of impulses. For this reason, it is frequently held that the loss of sensation following the administration of such agents as ether and chloroform, is due to the fact that the dissolution of the fatty material in nerve tissue induces a retraction of these filaments, preventing thereby the sensory impulses from reaching their respective afferent paths.

The Formation of Nerves and Their Distal and Central End-organs.—At a short distance from the cell-body the axone acquires a thick covering which is known as the

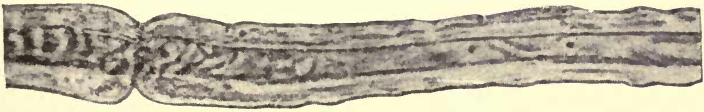


Fig. 41.—Medullated nerve fiber, showing nodes of Ranvier; × 660 times. (*Schäfer.*)

medullary sheath. Outside of this one lies a thin membranous investment which is known as the neurilemma. An axone or axis cylinder with its coverings constitutes a nerve fiber (Fig. 41). Many of these bound together into bundles, form a nerve. Accordingly, the cross-section of a nerve presents a membranous investment and numerous partitions of connective tissue, in the different spaces of which lie the individual nerve fibers. A nerve, such as the sciatic, embraces something like 300,000 fibers, each fiber attaining a diameter of about 10μ. This nerve, therefore, may be compared to a cable consisting of a large number of wires.

A collection of many cell-bodies within the central nervous system constitutes a *nucleus*. Thus, those cell-bodies which give rise to the axis cylinders of the vagus nerve, are collectively designated as the nucleus of the vagus. Similar well defined colonies of cell-bodies within or without the central nervous system are generally called *ganglia*. The spinal ganglion, for example, embraces a large number of cell-bodies, the sensory axones of which connect peripheral parts with the spinal cord. Whenever these collections of ganglion

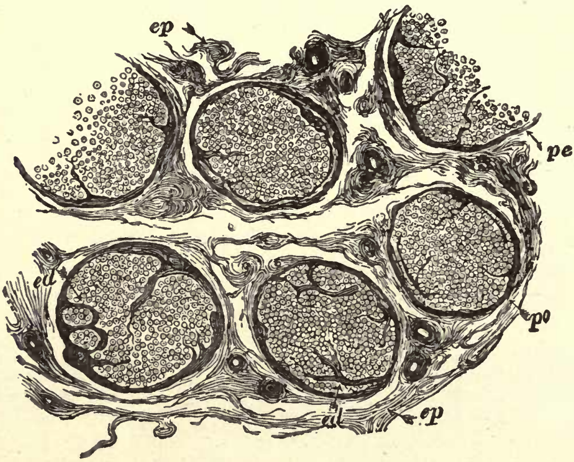


FIG. 42.—Transverse section of a nerve (Median). *Ep*, epineurium; *pe*, perineurium; *ed*, endoneurium. (*Landois and Stirling.*)

cells control a definite mechanism, they are said to form a *center*. We have previously noted that the movements of the skeletal musculature are controlled by a group of large nerve cells which are situated in the outer layers of the cerebrum next to the fissure of Rolando. Since these cells subserve this particular function, they may be said to form the motor center for muscular action. Similar groups of ganglion cells are found in different parts of the central nervous system. Our attention should be directed at this time to those situated in the upper portion of the spinal cord or medulla oblongata. These cells appear in three principal

groups which severally control the action of the heart, the caliber of the bloodvessels, and the respiratory activity. In other words, they constitute the so-called cardiac, vasomotor and respiratory centers.

If we now follow the course of the sciatic nerve to distant parts, we find that its individual axones finally lose their investing sheaths and break up into numerous fine filaments, each terminating in a structure known as an *end-organ*. As

Fig. 43.—End-plates; chlorid of gold preparation to show the axis cylinders and their final ramifications of fibrillæ. × 170. (*Szymonowicz*.)

has been emphasized above, the sciatic nerve contains efferent as well as afferent fibers. The former convey impulses into the end-organs, and the latter reversely into its nucleus or center. It is to be noted especially that the end-organs of the motor fibers differ very markedly in their structure from those attached to the sensory fibers. To simplify matters, let us suppose that a mechanical impact is brought to bear upon the skin of the foot which eventually gives rise to a contraction of the muscles of this part. This impact is received by a specialized sense-organ which is known as a

receptor, and is then conveyed in the form of an afferent impulse to the center. Here it gives rise to an efferent impulse which is conducted outward into the motor end-organ or *effector*, activating the corresponding muscle fibers (Fig. 40).

These receptors and effectors possess a very characteristic structure. Ordinary impacts of touch are received by the so-called tactile corpuscles of the deeper layer of the skin. These particular receptors appear as a rule as bulbular enlargements of cells, the core of which is occupied by the terminal nerve fiber. If we observe for a moment the tactile corpuscle illustrated in Fig. 44, it will be apparent that the

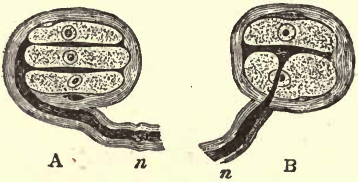


FIG. 44.—Corpuscles of Grandry from the duck's tongue. (*Izquierdo*.) *A*, compound of three cells, with two interposed discs, into which the axis cylinder of the nerve, *n*, is observed to pass; in *B* there is but one tactile disc enclosed between two tactile cells.

displacement suffered by the skin in consequence of the impact must lead to a similar change in this receptor and a mechanical excitation of the nerve filament in its interior. An afferent impulse is the result of this stimulation.

The effector in skeletal muscle tissue presents itself as a bulbular ramification of nerve fibrils upon the sheath of the muscle cell. The term *motor-plate* is usually employed when reference is made to this formation. It is not to be supposed, however, that a muscle composed of say 100,000 cells, is supplied by an equal number of nerve fibers. Since the axis cylinder of each fiber divides into a large number of fibrils, each of which ramifies, one axone may supply as many as one hundred of these structures.

It is to be remembered, however, that we have described at this time merely one particular kind of receptor. Many others could still be mentioned, for example, that of the retina of the eye which receives the ethereal impacts of

light, the organ of Corti of the internal ear through which the sound waves gain psychic recognition, the taste-buds which receive the chemical stimuli giving rise to the sensation of taste, and the olfactory cells which interact with the odoriferous particles of the air to produce the sensation of smell. The motor end-organ of smooth muscle possesses a structure similar to that found in skeletal muscle.

The Physiological Properties of a Nerve.—Under normal circumstances an efferent neurone is activated through its center, and an afferent neurone through its receptor. Under experimental conditions, however, it is possible to stimulate a neurone at any point of its course. Consequently, inasmuch as a nerve represents a collection of axones, its sole function must be to conduct impulses away from the area in which they are generated. The element chiefly concerned with this function is the axone or axis cylinder. Neither the medullary substance nor the neurilemma appear to be directly involved in this process of conduction, because many nerve fibers fulfill their function perfectly, although not in possession of a medullary sheath nor neurilemma. While this fact has been clearly established, the function of these envelopes has not been definitely ascertained as yet. But, inasmuch as a nerve fiber presents the essential characteristics of an insulated wire, it has been supposed that the medullary substance is insulatory and protective. This contention, however, cannot be substantiated, because the fibers of the sympathetic system are all non-medullated. Neither is it correct to ascribe to it a nutritive function, because the axis cylinder receives its nourishment directly from the cell-body by a process which may be likened to protoplasmic streaming.

Nervous tissue possesses a high degree of irritability and conductivity. For this reason it is frequently referred to as the master tissue of the body. When its component cells are stimulated, it yields a peculiar wave of excitation or irritability which traverses its different conductile segments and is here clearly recognized as a variation in their electrical potential. This wave constitutes the nerve impulse. The only indication of the activity of a nerve or of the

passage of a nerve impulse is presented by this electrical variation.

Probably the first idea that one might form regarding the nature of the nerve impulse, embodies the principles of the conduction of an electrical wave through a metal conductor. Electricity is not matter, but merely a form of energy. It does not actually pass onward like water through a tube, but presents itself as a change in a constant physical force. It must be admitted that a nerve impulse shows similar characteristics, but since its speed is very much slower than that of an electrical current passed through a copper wire, these processes cannot justly be said to be identical. Furthermore, a metal conductor may convey innumerable electrical waves without showing the slightest deterioration or destruction of its substance. To a certain extent this is also true of nerve-fibers, because they do not exhibit easily recognizable signs of metabolism and fatigue. When, however, a nerve is placed in an atmosphere deficient in oxygen, it soon ceases to conduct impulses. Lastly, it is to be noted that it liberates carbon dioxid when stimulated.

These observations strongly suggest that conduction in nerve is associated with definite catabolic changes. Hence, since catabolic processes must always be followed by anabolic processes in order to prevent cellular exhaustion, it may be surmised that a certain period of time must always elapse between the successive states of activity of the nerve during which it can rebuild its substance. The fact that such changes actually occur in nerve tissue, is substantiated by the observation that quickly repeated stimuli eventually fail to excite impulses. Nerve fibers, therefore, possess a definite refractory period during which they are impermeable to stimuli, but this period is extremely short, amounting to only about 0.006 of a second.

It must be granted, however, that the activity of nerve does not lead to an appreciable destruction of its substance, and that whatever dissimilation takes place is quickly remedied. The briefness of the refractory period of nerve fully proves this statement. Contrariwise, the cell-bodies and end-organs reveal a very intense metabolism and can,

therefore, be fatigued with much greater ease. It has previously been shown that an excised muscle, if stimulated excessively, soon loses its irritability and contractility. A condition of this kind, however, cannot be reproduced in the normal body, because its muscles are protected against complete fatigue by the end-plates. The latter are easily fatigued, and cease at this time to transfer the impulses to the muscle substance. On account of their greater vulnerability they serve, so to speak, as safety-valves for the muscle.

These data clearly prove that the basis of the nerve impulse is formed by definite chemical changes. It is true, however, that the latter are associated with an electrical variation which may be detected with the aid of almost any suitable indicator, such as a galvanometer. If an instrument of this kind is connected with a nerve, the stimulation of the latter gives rise to very characteristic deflections of its recording needle. This is the method usually employed to prove that nerve fibers are actually conductile, although their functional power may also be tested by observing whether their excitation elicits motor effects, such as the contraction of a muscle. Consequently, a nerve impulse may be defined as a metabolic wave in neuroplasm which is accompanied by an electrical variation. It has been ascertained that this wave progresses in the nerves of warm-blooded animals with a speed varying between 100 and 125 m. in a second.

The preceding definition immediately disposes of the assumption that the nerve impulse is a pulsation in neuroplasm, such as may be produced in a rubber tube filled with water by sharply tapping upon its wall. Nerves are not hollow tubes, nor is neuroplasm a fluid. Neither is it permissible to liken nerves to irritable strings of tissue, and to state that a nerve impulse results whenever these sensitive fibers are pulled upon. To be sure, we frequently characterize certain sensations as "nerve-tension" and "nerve-strains," but these sensory manifestations have their origin in the receptors of the skeletal muscles and not in the nerves themselves.

Reflex Action.—If an amœba or other unicellular organism is touched, certain specialized reactions ensue in its substance

in consequence of this impact which will carry it away from the seat of the stimulation. Likewise, if a mechanical stimulus of sufficient strength is applied to the skin of one of our hands, the muscles of this part contract, thereby giving rise to a particular movement. The principle involved in these reactions is essentially the same, because the stimulus is followed in each case by a motor action. It is to be noted, however, that the reactions in the amœba are accomplished without nervous tissue, while those in us require the presence of this tissue.

The Animal Kingdom embraces certain types of organisms which are in possession of nervous elements and certain types which are not. The former may again be divided into two groups, this division being based upon the structural and functional development or complexity of this tissue. All the higher animals are equipped with ganglion cells which subserve volition and other psychic manifestations. For this reason, they are able to control their motor responses by volition, while the lower forms are not. In accordance with this general outline, the motor reactions in the animal world may be arranged in three groups, namely as:

(*a*) reflex-like actions, or reactions effected with the aid of ordinary protoplasm,

(*b*) reflex actions, or reactions accomplished by means of nerve tissue, but without the intervention of the will, and

(*c*) volitional actions, or reactions brought about with the help of nervous tissue and closely controlled by the will.

The higher animal, however, also presents many non-volitional reactions or reflexes, in addition to its volitional ones. Thus, it need scarcely be mentioned that our skeletal musculature is under the control of the will, whereas the movements of our stomach, intestine, and urinary organs are not. Inasmuch as the function of the central nervous system is more difficult to understand than that of the circulatory or respiratory system, it seems advisable to postpone the discussion of this subject-matter until the student has acquired a knowledge of the simpler phases of physiology. Reflex action, on the other hand, plays a most important part in the production of all motor responses and, hence, it seems

essential that the student obtain a clear idea regarding its possibilities before endeavoring to analyze the phenomena connected with the circulation of the blood, the movements of respiration, and other functions.

We have seen that the most elementary structural unit of the nervous system is the neurone. Quite similarly, it may be held that the reflex act constitutes the most elementary functional unit of this system. It is an act executed in response to a stimulus without attention or volition. This definition implies that the stimulus is converted into a reaction without being first subjected to an association in the higher centers of the cerebrum. On this account, the reflex act bears a close resemblance to the reaction shown by simple masses of living matter, although it requires conduction through nervous tissue.

The example usually given to illustrate reflex action is the following: If the hand of a person is accidentally brought in contact with a hot object, it is instantaneously withdrawn from the seat of the stimulation. It may then be held that the person felt pain and withdrew the hand in consequence thereof by the volitional contraction of certain muscles. This explanation, however, is not correct, because it can easily be proved that the response was completed before the pain was actually perceived. Hence, the psychic centers could not have influenced this act, and the muscular response could not have been evoked volitionally.

As another example might be mentioned the constriction and dilatation of the pupil. If we gaze through a window, the size of this orifice is diminished in consequence of the contraction of that layer of smooth muscle tissue of the iris which is arranged circularly in its substance. Contrariwise, low intensities of light give rise to a contraction of those smooth muscle cells which permeate it radially inward from its periphery. The edge of the iris is then retracted, and the size of the pupil increased. It need scarcely be mentioned that this action on the part of the iris varies the size of the bundle of light which is permitted to enter the interior of the eye. It cannot be influenced by attention nor volition and hence, is a simple reflex act.

Other familiar reflexes are the acts of coughing and sneezing which serve to protect the respiratory passage against the entrance of foreign bodies. In these instances, the excitation of the lining membrane of the nose or pharynx gives rise to a forced expiration and a powerful blast of air which is intended to remove the stimulus.

In order to be able to obtain these elementary nervous reactions at least two neurones must be present: namely, a sensory one and a motor one. Their union is effected in the synapse. The neurone which conveys the impulse from the receptor to the center, constitutes the afferent path of this circuit, and the one conducting the impulse from the center to the effector, its efferent path. Stated in detail, a simple reflex system invariably embraces a receptor, an afferent path, a center, an efferent path, and an effector.

PART II

THE CIRCULATION OF THE BLOOD AND LYMPH

CHAPTER X

THE LYMPH

General Characteristics of the Body-fluids.—Every cell contains a certain quantity of water and a certain amount of solids. This is true of free-living cells as well as of those constituting the different tissues and organs of the higher animals. Roughly speaking, it may be said that the relationship between these constituents is as 3:1, *i.e.*, three parts of water and one part of solids. It is true, however, that cells differ somewhat in this respect, showing a water content of 65 to 79 per cent. in the different tissues. As might be expected, the blood is very rich in water. It contains only 21 parts of dry solids, and of these almost 12 parts are apportioned to its corpuscular elements.

In the lowest organisms specialized circulatory fluids, such as the blood and lymph, are not present. The substance of these forms is permeated by a fluid which is composed chiefly of water and is designated as the body-fluid. The composition of this fluid is not very different from that of the surrounding medium, because it is separated from the latter by only a delicate membrane which permits free osmotic interchanges. The nutritive substances and respiratory gases diffuse through this membrane in either direction.

The body-fluid is able to acquire a higher concentration and differentiation only when these interchanges with the outside medium are somewhat restricted. This stage of development is attained by those organisms which, on

account of their size and complexity, do not interchange solely through their enveloping membrane, but principally through a membranous tube which traverses the entire body and is known as the celom or alimentary canal. This channel is beset with many smaller tubules and recesses which extend into the outlying colonies of cells and bring the latter into closer relation with their sources of nutritive supply. In the animals of somewhat greater complexity, these recesses are separated from the main body-cavity and form a series of spaces containing a fluid which, on account of its greater isolation, is able to acquire and retain a much more characteristic composition. These elementary spaces form the beginning of the circulatory system of the higher animals.

The fluid occupying the intercellular spaces of the lowest forms, is shifted in consequence of the general movements of the organism. In the higher forms, on the other hand, it is propelled through an extensive system of separate channels by means of a highly specialized pumping organ which is known as the heart. Because of its imparted motion, the blood is in the best possible position to play the rôle of a middleman whose duty it is to convey nutritive particles to the distant cells and to relieve the latter of their waste products. We shall see later that it is able to fulfill this function very efficiently, because it comprises different cellular elements, each of which has a particular purpose to fulfill.

Another very excellent provision is that all the higher animals are equipped with two types of body-fluids, which are severally designated as the blood and lymph. The former is a much more complex medium than the latter, because it contains in addition to the plasma a large number of separate cells of different size and shape. The arrangement usually followed in the construction of a tissue is this: Every cell is surrounded by intercellular material which possesses a lesser density than its cytoplasm and nuclear material. For this reason, it is commonly stated that the different tissue cells are bathed in lymph. This fluid consists of a large amount of water in which the different substances required by the cells are dissolved. As far as its

general character is concerned, it approaches, therefore, most closely the ordinary body-fluid of the lowest forms. Furthermore, since the cells constantly interchange materials with the blood through this particular medium, it forms an important functional link between these two systems.

The interposition between the complex blood and the cells of so simple a medium as the lymph is of the greatest economic value. It must be evident that a much greater number of blood-channels and a very much larger quantity of blood would be required if this provision had not been made. Clearly, the lymph furnishes a very simple means of bringing every cell into direct functional relation with the blood. Owing to its wide distribution, it is possible to restrict the quantity of the blood without endangering the life of the cells.

The Formation of the Lymph.—The channels of the blood vascular system eventually divide into a multitude of very small tubules which are known as capillaries. These finest ramifications of the vascular system are limited by a wall of very thin, plate-like cells of endothelium. External to this lining are situated the different cells of the tissues. A thin layer of lymph is interposed between the latter and the walls of the capillary. As the blood traverses these small tubules, a portion of its fluid part or plasma is transferred into the intercellular lymph-spaces, but since its formed elements as well as larger nutritive elements cannot get through, the lymph is really diluted plasma. It is to be remembered, however, that its formation is not due solely to mechanical factors, such as differences in pressures, but also to osmosis, diffusion, and certain chemico-physical activities of the lining cells, the nature of which is as yet not fully recognized.

It may then be asked whether this portion of the blood plasma which has been diverted into the spaces between the cells, is actually lost to the blood. A glance at Fig. 45 will show that it is not, because the lymph spaces are united into very delicate tubules and these in turn into ducts, until eventually a main collecting tube has been formed which opens directly into one of the central veins. Having in this

way regained the blood vascular system, the lymph is again forced into the peripheral vessels as a part of the plasma.

It will be seen, therefore, that the tissues of our body are permeated by two sets of tubules: namely, those belonging to the blood vascular system and those constituting the lymphatic system. If the surface of the skin is slightly scraped, a number of fine droplets of a watery fluid will be seen to

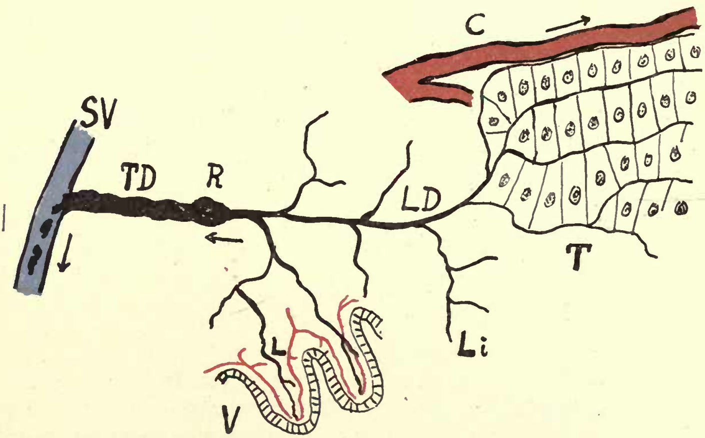


FIG. 45.—Scheme of the circulatory system of the lymph. *C*, blood capillaries; *T*, tissue cells; *L.D*, lymphatics; *L*, lacteals; *V*, villi of intestine: *Li*, liver; *R*, receptacle; *T.D*, thoracic duct; *S.v*, subclavian vein.

escape from the opened lymph ducts. These droplets of lymph finally coalesce and coagulate, forming a thin film over the injured area. But, if the skin is incised more deeply, a certain number of blood-capillaries will also be opened which discharge their contents into the extravasate, imparting to it a distinct reddish color. Since the blood also possesses the power of clotting, a common coagulum will eventually result.

The Distribution of the Lymphatic Channels.—The walls of the finest lymphatic tubules are composed of thin, plate-like cells and present, therefore, a structure very similar to that of the blood-capillaries. The larger ducts, on the other hand, are strengthened by a certain amount of connective

tissue, and acquire a diameter of several millimeters. It is also of interest to note that the orifices of the smaller lymphatics are guarded by valves which usually consist of two cup-shaped flaps directed toward the larger tubule. They close immediately if the pressure in the more central lymphatic rises above that prevailing in the more distal channel. In this way a back flow is made practically impossible.

The lymphatic channels are beset at frequent intervals with rounded glandular structures, the so-called *lymph-nodes*. Small amœboid cells are formed in these nodular bodies which are known as *lymph-corpuscles* or *lymphocytes*. These cells

FIG. 45*a*.—Cross-section of lymphatic vessel to show arrangement of valves.

are flushed into the bloodstream, where they change into the white cells of the blood and may also be transferred into leukocytes. The lymphatic glands also play the part of filters, retaining any foreign substance that may have entered the lymph-stream. For this reason, it is frequently noted that micro-organisms are held back in these sieve-like structures, evoking here an inflammatory reaction and causing them to become enlarged and painful to the touch. In many cases, a general inflammation of the lymphatics then results, causing them to become sharply outlined against the integument as delicate, bright red threads which extend from the infected area toward the next colony of lymphatic glands. If the infectious material is particularly virulent, it may succeed in getting beyond these peripheral stations, but may again be effectively blocked by the glands situated farther centrally. A general infection of the body results only if all these stations have been passed successively.

As has been stated above, the main collecting channels discharge their contents directly into the venous bloodstream. The largest of these is the thoracic duct which joins the venous system at the point of confluence of the external

jugular and left subclavian veins, and drains the legs, abdominal organs, and entire left side and lower half of the right side of the chest. In man it is 38 to 45 cm. in length and of

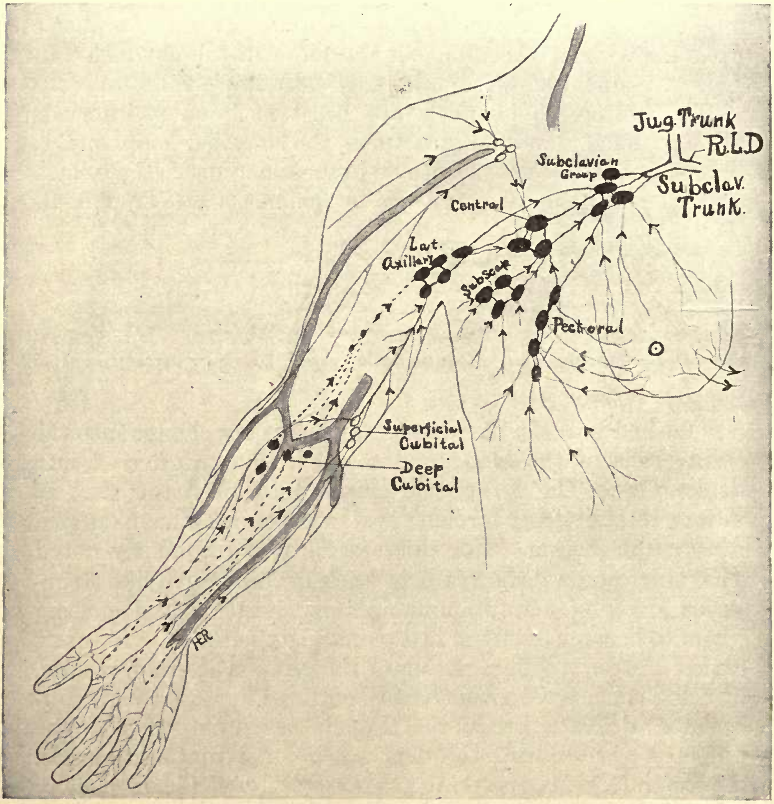


FIG. 46.—Lymph nodes and lymphatic drainage of the upper extremity, mammary gland and thoracic wall; *RLD*, right lymphatic duct. (*Radasch.*)

about the size of a goose quill. It lies to the left of the spinal column and thoracic aorta. A separate duct, about 2.5 cm. in length, is provided for the upper right side of the chest. Separate channels which are known as the right

and left cervical lymphatics, return the lymph from the neck and head.

On account of their small caliber and watery appearance of their contents, the distal lymphatics cannot be made

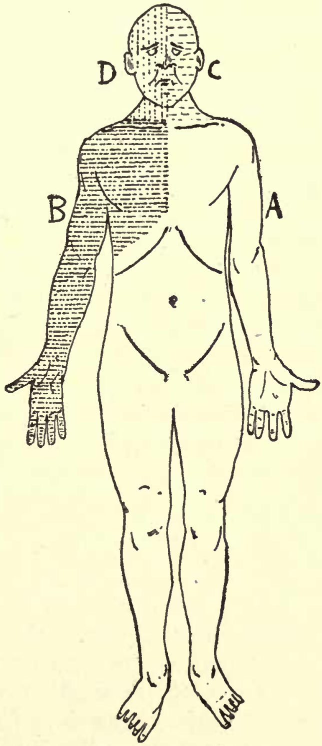


FIG. 47.—The distribution of the lymphatics. *A*, The domain of the thoracic duct (unshaded portion); *B*, right lymph duct; *C*, left cervical duct; *D*, right cervical duct.

out with great ease, while those of the intestine are very sharply outlined whenever fat is being absorbed. It will be shown later that by far the largest portion of the digested fat attains the blood through the so-called lacteals which form the finest radicles of the lymphatic system in this organ.

8

These lacteals are situated within small finger-like projections of the mucosa which are known as villi. After the fine globules of fat have entered these tubules, they impart a milky appearance to the lymph contained therein, so that each lymphatic may readily be traced from its very beginning to its point of confluence with the thoracic duct. Lymph containing large amounts of fat is known as **chyle.**

The Flow of the Lymph.—The factors which may be held responsible for the return of the lymph, are:

(*a*) *Differences in Pressure.*—The lymph is formed under the pressure prevailing in the blood-capillaries. It amounts to about 40 mm. Hg. In the venous system, on the other hand, the pressure is below that of the atmosphere, and amounts to about -5 mm. Hg. Accordingly, the pressure throughout the lymphatic system decreases by about 50 mm. Hg, a difference equal to that which causes the venous blood to be returned to the heart.

(*b*) *Muscular Movements.*—Every contraction of our skeletal muscles exerts a mechanical influence upon the extremely soft walls of the lymphatics, pressing their contents onward.

(*c*) *Lymphatic Valves.*—Inasmuch as these membranous flaps open only in the direction of the veins, a backward flow of the lymph cannot take place.

(*d*) *Lymph-hearts.*—The lymphatics of certain animals are beset with pulsating organs which act in the manner of the blood-heart and establish definite pressures within their chambers. The orifices of the lymphatics leading into these secondary hearts are guarded by valves and are tightly closed during the period of contraction of these organs. They open when relaxation sets in. Contrariwise, the valve guarding the orifice of the collecting lymphatic opens during the phase of contraction and closes during the phase of relaxation. By this means the lymph is constantly forced onward in the direction of the veins.

(*e*) *Suction-action.*—Inasmuch as the principal lymphatic enters the vein at almost a right angle, the lymph is actually drawn into the venous channel.

CHAPTER XI

THE BLOOD

Composition and General Characteristics.—The blood is a viscous fluid, consisting of a watery portion or plasma and various solids. The latter are held in solution as well as suspension, and embrace different nutritive substances and a large number of formed elements which are known as corpuscles. The corpuscular portion consists of red cells (erythrocytes), white cells (leukocytes), and platelets (thrombocytes).

- Blood
  - Water
  - Solids
    - dissolved nutritive substances
    - larger nutritive particles
    - Corpuscles
      - red, erythrocytes
      - white, leukocytes
      - platelets, thrombocytes

Plasma

When present in larger amounts, the blood of the mammals exhibits a very characteristic color, varying between scarlet red and purple. This difference is due to the fact that the amount of oxygen contained in the pigmentous material of the red cells is greatest in the arterial blood and least in the venous blood. It is evident, therefore, that the color of the blood must be of distinct value to the physician, because it betrays the degree of oxygenation of the tissues. A low content in oxygen invariably suggests itself by a bluish color of the exposed parts, such as the lips and skin of the face. Single red corpuscles, however, possess a yellowish color, and a distinct reddish hue is imparted to the blood only when these elements are present in considerable numbers.

Blood possesses a salty taste and faint odor. Its specific gravity is about 1.055. Its temperature varies in different parts of the body, being highest in those vessels which are well protected by the tissues, and lowest in those situated near the surface. Thus, the blood in the veins of the liver may attain a temperature of 39.7° C. (103° F.), while that in the fingers, nose, and cheeks may possess a temperature of only 36.0° C. (97.7° F.). Naturally, the blood receives its heat from the cells of the different tissues and transfers it later on to the air either by radiation or in the form of bound heat. The source of this heat, therefore, lies in the oxidations of the tissue cells.

The Distribution and Total Quantity of the Blood.—The total quantity of blood present in an animal may be measured in different ways. The method most easily followed is the one which purposes to collect all the blood by simply opening a large artery and permitting its contents to flow into a graduated receptacle. This procedure, however, is by no means exact, because some of the blood always remains in the veins and capillaries and cannot be expelled by the force of the heart beat. Much more valuable data have been obtained by the chemical and colorimetric methods. While these procedures cannot be described in detail at this time, it may be of interest to note the values which have been ascertained with their aid. The earlier determinations have placed the blood-volume of the human subject at about 5 liters. More recently, however, it has been found that any calculation made upon the basis of $\frac{1}{13}$ of the body-weight, is too high, and that a volume of about 4 liters or 9 pounds is much nearer the correct value. This statement implies that the total quantity of the blood amounts to $\frac{1}{17}$–$\frac{1}{20}$ of the body-weight. The latter figure should be employed for these calculations if the weight of the person is augmented by a heavy deposition of fatty tissue.

After the blood has been ejected from the heart it is distributed to the different organs of the body in amounts corresponding to their activity. Obviously, the bones, tendons, and cartilages require only a very small amount of nutritive material, because they do not undergo intense metabolic

changes after they have attained their full development. Glandular tissues, on the other hand, are very active and must, therefore, be in possession of a constant supply of material from which their products can be formed. Accordingly, it is found that such organs as the kidneys, brain, and glands of internal secretion are in constant need of copious amounts of blood. The thyroid, for example, receives 560 c.c. of blood in a minute per 100 grams of substance, while the connective tissue structures of the head obtain only 5 c.c. in a minute for the same weight of substance.

If we would suddenly ligate different bloodvessels so as to divide the body into several separate vascular areas, we would find that one-quarter of the total amount of blood is contained at any one time in the heart, lungs and large vessels, one-quarter in the liver and portal vessels, one-quarter in the skeletal muscles, and one-quarter in the remaining organs.

The Red Corpuscles.—If a small drop of human blood is collected upon a glass slide and is placed under the ocular

FIG. 48*a*.—Human red corpuscle placed flat and on edge.

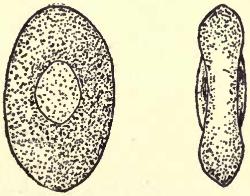


FIG. 48*b*.—Red corpuscle of frog placed flat and on edge.

of a microscope, it will be seen to contain a very large number of cellular elements, among which the red corpuscles or erythrocytes are the most conspicuous. These bodies appear as flattened, circular discs, possessing a diameter of 7.6μ ($\frac{1}{3200}$ of an inch), and a thickness of about 2μ. It will be noted that the central area of each cell is much thinner than its marginal one and hence, its cross-section must exhibit the general outline of a dumbbell. In seeking an explanation for this structural peculiarity, it should be

remembered that the human red cell loses its nucleus very soon after its formation and enters the circulatory system non-nucleated.

An exception to this rule results only when the corpuscle-forming organs are in a state of the highest possible activity in order to replace cells which have been lost by bleeding or other destructive processes. In this connection it should also be mentioned that these corpuscles are developed during adult life in the red marrow of the bones. Their mother-cells are the so-called erythroblasts of the red marrow. This fatty material occupies the extremities of the long bones, while their shafts are filled with yellow marrow. Whenever a rapid destruction of red corpuscles has taken place in consequence of a hemorrhage, the red marrow increases in mass at the expense of the neighboring yellow marrow. This change is also well illustrated by the hibernating animals which undergo very decisive metabolic changes at the beginning of spring, and again late in the autumn. When their increased bodily activity suddenly calls for a greater number of red corpuscles to take care of their extra demand for oxygen, the red marrow rapidly increases in bulk. The reverse change takes place when the metabolism of these animals is gradually reduced to its low standard of the winter months.

Under ordinary circumstances, the human red corpuscles are destroyed in constant numbers. They become senile while circulating, and are subsequently broken down in the liver, their remnants being here employed in the formation of the pigments of the bile. This steady destruction must be compensated for by a constant formation.

The red blood-corpuscles of the cold-blooded animals are elliptical in shape and retain a very conspicuous nucleus throughout their life. Those of the frog measure 25μ in length and 15μ in breadth, and are, therefore, more than three times as large as the human red cell. Still larger corpuscles are found in the salamanders, where they attain a length of about 75μ.

The number of the red corpuscles varies with their size. Thus, the frog possesses only about 1,500,000 red cells in

each cubic millimeter of blood, whereas human blood contains about 5,000,000 in this amount. Accordingly, the total number of red cells present in a person weighing about 150 lbs. must be something like 20 trillions. In this connection, brief reference should also be made to the fact that the people inhabiting high regions possess a larger number of red corpuscles than those living at lower levels.

Each red cell consists of a delicate saccule, in the interior of which is contained a substance known as *hemoglobin*. In reality, therefore, the red cell may be regarded as a tiny mass of hemoglobin which possesses the peculiar property of uniting with the oxygen of the atmospheric air. By virtue of its affinity for this gas, this constituent confers upon the red corpuscle its characteristic function of an oxygen carrier. On leaving the capillaries of the lungs each red cell is fully loaded with this gas. Its hemoglobin is then in the form of oxy-hemoglobin, *i.e.*, completely charged with oxygen. In the tissues, a part of this gas is transferred to the cells to enable them to oxidize their nutritive substances. Hemoglobin so partially depleted of its store in oxygen, is called reduced hemoglobin. These differences are responsible for the variations in the color of the blood. The arterial blood is bright red, because it contains large amounts of oxygen, whereas venous blood is purplish, because it embraces smaller quantities of this gas.

In accordance with the foregoing discussion, it may be concluded that any reduction in the number of the red corpuscles or any diminution in the hemoglobin content of the individual red cells must greatly diminish the oxygen carrying capacity of the blood and finally lead to an improper aeration of the tissues. The term "*anœmia*" signifies that the blood contains an abnormally small number of red cells, possibly only two to three millions to the cubic millimeter. This condition may have its cause either in a decreased production or an increased destruction of these corpuscles. As causative agents of it might be mentioned: an excessive loss of blood, circulating toxins and poisons, amœba and filiaria infections of the intestines and blood, and a general unhygienic mode of life. The term *chlorosis* suggests that the hemo-

globin content of the blood is below normal. This condition is usually associated with anæmia, because a decided reduction in the number of the red cells must also diminish the total amount of hemoglobin, although each red corpuscle may still be in possession of its necessary quantity of hemoglobin. It may also happen that the hemoglobin content of each red cell is lower than it should be, although the total number of these elements is practically normal. It should be remembered, however, that distinct disturbances arise only when the hemoglobin falls below 80 per cent. of normal, and that even perfectly normal persons rarely show a hemoglobin content of 100 per cent.

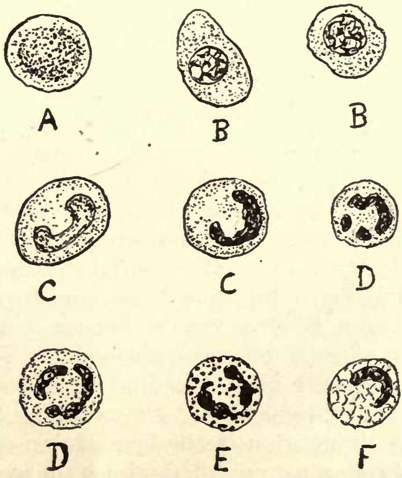


FIG. 49.—Different varieties of human white corpuscles. *A*, lymphocyte; *B*, mononuclear leukocyte; *C*, transitional form; *D*, polynuclear leukocyte; *E*, eosinophile leukocyte; *F*, mast-cell. (*After Szymonowicz.*)

The White Corpuscles.—The colorless corpuscles of the blood vary greatly in size. The smaller ones possess a diameter of only 4μ, while the larger ones may attain a diameter of 14μ. Both types of cells are irregular in outline, because they possess amœboid powers and alter their contours constantly. The larger ones, which are known as leukocytes, exhibit the most decided changes. When

placed under the ocular of a microscope, yielding a magnification of about 500 diameters, they may be seen to send out delicate processes in particular directions, meanwhile retracting their protoplasm elsewhere. In this way, they are able to proceed from place to place, but, naturally, their movements are slow and require minutes for their completion. When in the bloodstream, these cells are usually found in the outer clear zone of the plasma, where they attach themselves to the wall of the vessel. Every now and then, however, they become detached and roll on to more distant parts of the vascular system. Their number varies between 6000 and 10,000 to the cubic millimeter of blood and, hence, their proportion is as 1:700 red cells.

These amœboid qualities are responsible for the power of the leukocytes to surround and destroy foreign particles that

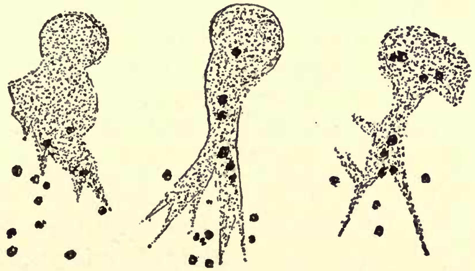


Fig. 50.—Leukocytes engulfing particles of India ink.

may have entered the bloodstream. This process which is known as *phagocytosis*, constitutes one of the most important safeguards of the body against invasion by bacteria. In this connection it should also be noted that these cells are able to attach themselves firmly to the wall of the bloodvessel and to perforate it in order to gain access to the neighboring tissues. This migration is the natural consequence of the invasion of the body by pus producing bacteria. Thus, if a colony of these micro-organisms has succeeded in finding lodgment in the deeper layers of the skin, the leukocytes are attracted to them in a chemical way. They leave the bloodvessels and enter the tissues, where they engulf and digest

this toxic material. Accordingly, the leukocytes may be said to serve the purposes of policemen, because they are in evidence everywhere as safeguards against microbic invasion. They are greatly aided in the performance of this important function by certain changes in the character of the bloodstream which materially facilitate their movements. Thus, supposing that a certain region of the body has become the seat of an infection, it will be noticed that:

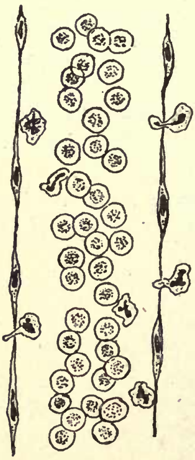


Fig. 51.—Migration of leukocytes.

(*a*) The bloodvessels of this part relax, causing the speed of the bloodflow to be diminished and the total quantity of the blood to be increased. This change is responsible for the greater warmth and redness of the inflamed region.

(*b*) The leukocytes enter the vessels of this area in large numbers, attaching themselves everywhere to their walls. Having finally succeeded in perforating the lining cells, they migrate into the surrounding tissues.

(*c*) The leukocytes engulf and devour the bacteria. During this interaction many of them are killed, and are changed into the so-called pus-corpuscles, the principal constituent of pus. Inasmuch as an extra amount of lymph is at this time exuded into the inflamed tissues, their volume is increased. A certain pressure is then brought to bear upon the sensory nerve filaments situated among their cells with the result that the entire area becomes painful to the touch. It will be noted, therefore, that the four cardinal symptoms of an inflammation are: redness, swelling, heat, and pain.

The Blood Platelets.—These formed elements of the blood appear as irregular masses of protoplasm, possessing a diameter of only about 3μ. They consist of a dark center, representing in all probability the nucleus, and a small amount of cytoplasm which is arranged in the form of irregular pointed projections. They are very sensitive

and rapidly disintegrate when removed from their normal medium, the plasma. For this reason, they are rarely observed in blood collected in glass receptacles, although they may be preserved for some time in agar jelly or in solutions of magnesium sulphate. The blood of the frog, fishes, and birds does not contain these elements.

It has been shown that the platelets play an important part in the coagulation of the blood. When disintegrating they liberate thrombokinase, an agent which, as will be shown later, is primarily responsible for this change. Those animals which are not in possession of blood platelets, contain a certain coagulating agent in their tissues. Consequently, their blood must clot as readily as that of the animals possessing these bodies, because in its escape from the vessel it must flow across the incised tissues and be impregnated with this substance. Contrariwise, if the blood of a frog or other platelet-free animal is collected in a receptacle without having previously come in contact with the tissues, it will not clot, because no coagulating substance has been added to it. Inasmuch as Man possesses not only blood platelets but also a certain amount of coagulating subtance within his tissues, he is especially well protected.

The Coagulation of the Blood.—Possibly the most striking characteristic of the blood is its power of changing its fluid consistency into one of semi-solidity. Under ordinary circumstances it remains perfectly fluid while traversing the vascular channels, but assumes a gelatinous state very shortly after it has been brought in contact with a foreign body. The platelets are then destroyed and liberate thrombokinase. This agent in turn incites those peculiar changes which gradually cause the blood to lose its fluidity. Now, since the blood may be brought in contact with a foreign object while still in the bloodvessels as well as after it has been shed, it is possible to recognize two forms of coagulation, namely, an *intravascular* one and an *extravascular* one.

When blood is allowed to flow into a beaker, it is at first perfectly fluid, but stiffens perceptibly after the expiration of about four or five minutes. The time intervening between the moment of its withdrawal and the moment when it

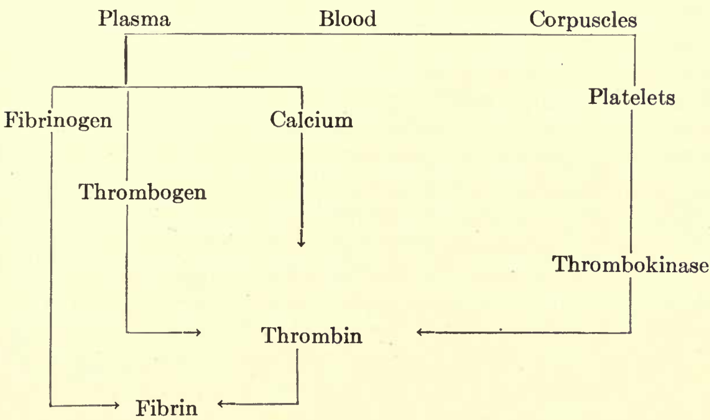
first assumes a gelatinous consistency, is known as the coagulation-time. While the length of this period varies somewhat in different animals and is subject to certain conditions, such as the temperature and carbon dioxid content of the blood and the size and smoothness of the vessel into which the blood is drawn, its average value may be said to be 5 minutes.

Brief reference should also be made at this time to the fact that the blood of some persons does not clot until after the expiration of a much longer period than the one just given. Whenever the coagulation-time is unduly prolonged, so that the person would really be in danger of suffering an excessive loss of blood even after a slight injury, he is said to be a bleeder or hemophilic. The cause of this condition of *hemophilia* is not known. Peculiarly enough, it affects only the males of a particular parent, destroying them as a rule before they have reached middle age. The females are exempt, but may propagate this characteristic to their children. The males of the second generation are subject to the same difficulties, while the females survive. In many instances these severe hemorrhages take place without any apparent cause and are repeated at intervals until life has been terminated.

The clotting of the blood is due to the production of fibrin, a complex substance which appears in the form of delicate threads permeating the blood in all directions. These filaments arise in the different colonies of disintegrated blood platelets which have been deposited upon the sides of the receptacle. In their progress through the blood they envelop the red and white corpuscles, finally carrying them by gravity to the bottom of the receptacle. This mass of fibrin and entrapped corpuscular elements form the *clot* or *coagulum*. Above it lies the *serum*, *i.e.*, the blood plasma devoid of its formed elements and other substances used up in the process of coagulation.

Fibrin is derived from fibrinogen, a normal constituent of the blood. This conversion of the inactive fibrinogen into the active fibrin is brought about by a complex ferment-like substance, known as thrombin. The latter in turn is derived

from thrombogen, a normal but inactive constituent of the blood. The activation of the latter is accomplished by thrombokinase in the presence of calcium. As is indicated in the accompanying table, the destruction of the platelets or thrombocytes liberates thrombokinase which in turn changes the thrombogen into thrombin, but only in the presence of calcium. The thrombin then converts fibrinogen into fibrin.



In accordance with the preceding discussion, it may be concluded that the circulating blood remains fluid because it is everywhere in contact with the normal intima of the bloodvessels. Obviously, the normal lining of the vessels is not destructive to its formed elements, particularly not the platelets. It may then be reasoned that any injury to the vascular channels, rendering a segment of a vessel abnormal, must lead to the coagulation of the blood, because the part of a vessel rendered abnormal by a stroke or chemical substance, must act as a foreign body and cause a certain number of platelets to collect upon it. Their disintegration then liberates thrombokinase which finally causes the formation of the fibrin threads. The latter entrap increasing numbers of red cells and leukocytes until a complete coagulum has been produced. A stationary intravascular clot is

known as a *thrombus*. The blood playing constantly against a thrombus may cause a piece of it to become separated from the main mass and to be forced onward into more distant circulatory channels. This *floating thrombus* or *embolus* may finally become lodged in one of the smaller tubules, causing an anæmia and functional uselessness of the cells normally supplied by this bloodvessel.

The Function of the Blood and Lymph.—The foregoing account must have shown that the blood and lymph possess practically identical functions, because they serve primarily the purpose of common carriers. As such they: (*a*) convey nutritive particles to the tissues and take the waste products away from them, (*b*) supply the tissues with oxygen and relieve them of their carbon dioxid, (*c*) serve as an osmotic medium in which these different interchanges are accomplished, (*d*) play an important part in the regulation of the body-temperature, (*e*) contain certain elements which protect the body against toxic material, and (*f*) distribute the products of the ductless glands to the different tissues.

CHAPTER XII

THE GENERAL ARRANGEMENT OF THE CIRCULATORY SYSTEM

Basic Principles of the Circulation.—Stress has previously been placed upon the fact that blood is a tissue, consisting of certain cellular elements, the corpuscles, and a certain quantity of intercellular material, the plasma. However, in order that this tissue may be able to fulfill the function of a common carrier, it cannot remain stationary but must move rapidly from place to place and eventually return to its starting point. Obviously, a complete circulation can only be established with the aid of three factors: namely, a system of recurrent tubes, a circulatory fluid, and a mechanism by means of which the latter is made to move. Since the function of the blood has been considered in detail in the preceding chapter, we are now in a better position to study those factors which enable it to complete its circuitous course through the different parts of the body.

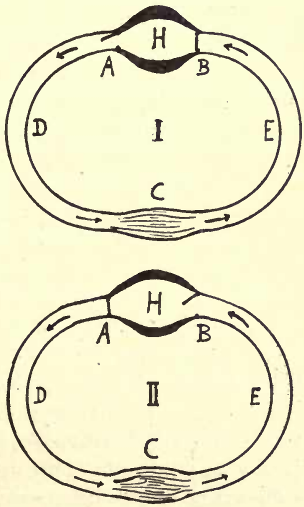


FIG. 52.—Schema of simple circulatory system. *I*, phase of contraction; *II*, phase of relaxation of heart; *A* and *B*, valves guarding cardiac orifices; *D*, arteries; *C*, capillaries; *E*, veins.

This subject-matter may well be introduced by a brief discussion of the fundamental laws pertaining to the movement of liquids as illustrated by Fig. 52. The heart which furnishes the driving force for the blood, first appears as a simple

enlargement of a certain segment of the vascular system. The walls of this segment are considerably thickened by the deposition of a special type of muscle cells possessing automatic qualities. This statement implies that this muscle tissue contracts rhythmically in consequence of an as yet unknown inherent cause. Now, inasmuch as this simple tubular heart is modelled after an ordinary rubber bulb, its alternate contractions and relaxations may be reproduced by compressing such a bulb at regular intervals in the palm of the hand. By inference it may be concluded that the contraction of the heart must lead to a decrease in its size, in consequence of which the fluid within it is placed under a higher pressure than that prevailing in the circular tube without. Accordingly, the fluid within the heart must seek a place of least resistance by escaping through orifices *A* and *B*. Later on, when this organ relaxes, the size of its chamber is increased and hence, the pressure within it must at this time be lower than that in the tube. The fluid then flows back into the heart through orifices *A* and *B*.

Clearly, a movement of this kind cannot be called a circulation, but represents merely an oscillatory shifting of the fluid. A true round-about movement, however, can easily be imparted to it if orifices *A* and *B* are equipped with valves, opening in the direction in which the circulation is to be established. This modification having been made, the rise in pressure resulting in the contracting heart must open valve *A* and close valve *B*. The fluid then leaves this central compartment through opening *A*. Contrariwise, the relaxation of the heart must close valve *A* and open valve *B*, thereby permitting the fluid to return through orifice *B*. In this way, every particle of the fluid is made to traverse the tube in its entirety and always in a direction from *A* to *B*.

In the normal circulatory system, the channels conveying the blood away from the heart are designated as arteries, and those returning it to the heart, as veins. The centralmost supply tube is commonly termed the aorta, and the centralmost collecting tube, the vena cava. It is also to be remembered that the arteries divide repeatedly into smaller tubes which are known as arterioles, and these in turn into

still finer tubules which are called capillaries. On the other side of this network of fine tubules lie the smaller collecting channels or venules. The latter finally unite into the veins, and these in turn into the vena cava.

Accordingly, the entire circulatory system may be divided into three parts: namely, into arteries, capillaries, and veins. In accordance with their size, these tubes may again be classified as arteries, arterioles, arterial capillaries, capillaries proper, venous capillaries, venules, and veins. It has previously been noted that any vessel conveying the blood away from the heart, is known as an artery and any vessel returning the blood to this organ, as a vein. Hence, the decisive factor in this terminology is the direction of the bloodflow and not the character of the blood. Thus, it is a well known fact that the pulmonary artery conveys venous blood to the lungs, while the pulmonary vein carries the thoroughly aerated blood from these organs to the heart. If it is desired, however, to make particular reference to the fully oxygenated blood, we may employ the adjective "arterial," whereas the adjective "venous" implies that the blood has lost a part of its oxygen.

The Elementary Heart.—In order to be able to obtain a concise idea regarding the action of the heart of the mammals, it seems advantageous to refer here briefly to a few data derived from comparative physiology. As has been stated above, the heart first appears as a simple bulbular enlargement of a particular segment of the general circulatory system. The muscle tissue composing its wall is automatically active, and furthermore, its orifices are beset with small membranous flaps which jointly possess the action of a valve. The tubular character of this organ is most conspicuously betrayed by the vermes. In these animals, the bloodvessels traversing the ventral and dorsal parts of the body, are connected by a number of lateral channels. The walls of the latter as well as those of the neighboring segment of the dorsal vessel, are automatically contractile. In this species, therefore, the heart extends over a large segment of the vascular system, and is distinctly tubular in its character.

Very similar conditions are met with in the amphibians and reptiles. The hearts of these animals also exhibit a tubular outline, but embrace three successive cavities which are connected with one another by large orifices. It is noted

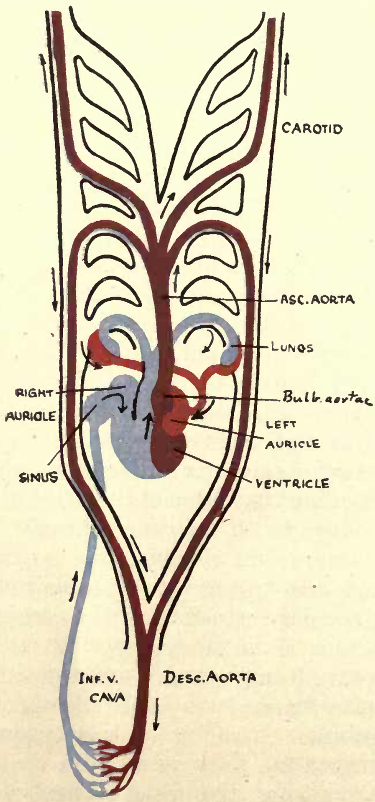


FIG. 53.—The circulation in the amphibians diagrammatically outlined.

first of all that the veins returning the blood from the different parts of the body, unite before they actually enter the heart, and form here a vestibule-like compartment which is known as the venous sinus. This chamber opens into the ante-

chamber of the heart or auricle, whence we pass into its main chamber or ventricle. The orifices connecting these different compartments, are guarded by valves which open only in the direction of the ventricle. Furthermore, the various segments of this heart do not contract simultaneously but successively, the sinus contracting first and the ventricle last. Consequently, the orderly flow of the blood through this organ depends upon two factors: namely, the successive contraction of the different cardiac segments, and the proper closure and opening of the valves guarding the aforesaid orifices. Regarding the second factor, it should be stated at this time that the contraction of the auricle closes the valve situated between this chamber and the sinus, but opens the one between it and the ventricle. Likewise, the contraction of the ventricle closes the auriculo-ventricular valve, but opens the one situated in the root of the aorta.

In accordance with the work performed by the different portions of this simple heart, it will be noted that their walls possess a different contractile power, as is indicated by their varying thickness. The walls of the sinus and auricles are thin, because the work demanded of them is comparatively slight. Their function is to pump the blood into the adjoining compartment, but this transfer is accomplished at a time when the receiving chamber is in the state of rest. The ventricle, on the other hand, drives the blood throughout the systemic vessels and must overcome the high resistance resident in these tubules. This end it can only accomplish by establishing a high initial pressure.

After its ejection from the heart, the blood enters a small cavity, the walls of which possess a certain contractile power in order to augment the action of the ventricle. This bulbular enlargement of the roots of the aortæ is known as the arterial bulb or bulbus arteriosus. Distally to it the two aortæ are seen to convey the blood to all parts of the body, but before leaving the immediate vicinity of the heart, these vessels give off two branches which lead to the lungs. By this means a portion of their contents is always diverted into the capillaries of these organs to be oxygenated. The blood is then returned to the left auricle by special vessels which

are termed the pulmonary veins. Accordingly, the circulatory system of the frog may be divided into a greater or systemic circuit and a lesser or pulmonary circuit. The former supplies the different tissues of the body, and begins with the aortæ. It terminates finally at the venous sinus. The latter originates with the pulmonary branches of the aortæ, and ends at the left auricle. The same general conditions prevail in the mammals, although in them the pulmonary artery arises directly from the right ventricle. Furthermore, the venous sinus does not appear in these animals as a separate cavity.

It need scarcely be emphasized that the perfectly open condition of the ventricular cavity permits the venous blood of the right auricle to intermingle with the freshly aerated blood of the left auricle. It is to be noted, however, that a thorough mixture between these two types of blood cannot take place, because the ventricle contracts immediately upon the completion of the contraction of the auricles. Moreover, since the oxygenated blood of the left auricle is collected in that portion of the ventricular cavity which lies nearest the aortæ, this type of blood must leave the heart first and follow the path of least resistance into the distal arteries. The succeeding gush of venous blood, on the other hand, must be retained very largely in the central segments of the aortæ, whence it is directed into the pulmonary arteries and capillaries of the lungs. It is evident, however, that a partial mixing of the oxygenated and venous types of blood cannot be entirely avoided in spite of this peculiarity in the distribution of the ventricular blood. Consequently, the systemic arteries cannot be supplied altogether with thoroughly aerated blood.

Very similar conditions prevail in the heart of the turtle. It is evident, however, that this organ is more solidly built than that of the frog in order to enable it to produce higher degrees of pressure. Furthermore, the aortæ and pulmonary artery arise directly from the ventricle as separate tubes. The ventricle itself is modified to show an at least partial separation into two cavities. This separation is accomplished by two membranous flaps which are brought together

at their edges during the period of contraction but again move away from one another during the subsequent relaxation of this portion of the heart. This partition serves the purpose of keeping the blood ejected by the left and right

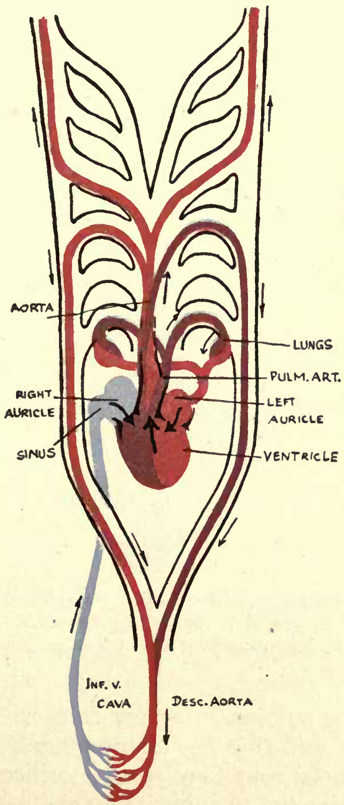


FIG. 54.—The circulation in reptilians diagrammatically outlined.

auricles apart, so that the former may be directed into the aortæ and the latter into the pulmonary artery.

The Complex Heart.—The heart of the adult mammal is divided by a median longitudinal septum into a right and a

left half. Each half is in turn divided by a transverse septum into an antechamber or auricle and a main chamber or ventricle. Accordingly, this organ consists of four chambers: namely, two auricles and two ventricles. The blood returned by way of the systemic veins is conveyed into the right auricle, while the blood from the lungs is directed into the left auricle. The two arterial channels leaving the heart arise from its ventricular portion, *i.e.*, the aorta from the left

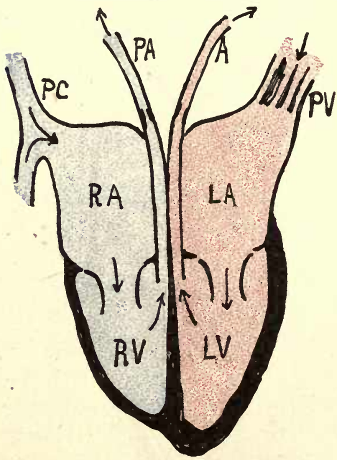


Fig. 55.—Diagram to show the course of the blood through the higher heart. *PC*, post cavæ; *RA*, right auricle; *LA*, left auricle; *RV*, right ventricle; *LV*, left ventricle; *PA*, pulmonary artery; *PV*, pulmonary vein; *A*, aorta.

ventricle and the pulmonary artery from the right ventricle. Thus, it may be said that the mammalian heart is in possession of two venous and two arterial orifices, although the caval and pulmonary openings are really formed by two tubes; in fact, in some animals four pulmonary veins are present.

Every globule of blood arriving in the right auricle passes from here into the right ventricle and thence into the pulmonary artery. After it has traversed the capillaries of the lungs it is returned to the heart by way of one of the pulmon-

ary veins. It reenters this organ at the left auricle, and subsequently traverses the left ventricle in order to reach the aorta. Distally to this channel, it follows the general course of the circulatory system and finally regains the heart by way of one of the vena cava.

Contrary to the conditions prevailing in the lower animals, the adult mammalian heart is constructed in such a way that an intermingling between the arterial and venous blood cannot take place. Hence, its left side contains scarlet red arterial blood, and its right side dark venous blood. This separation, however, is not established until after birth, because before this time a communication exists between the right and left auricles which allows the blood of the right cavity to escape into the corresponding compartment on the left side. But, inasmuch as the lungs of the mammals are absolutely inactive before birth, we cannot justly speak of an intermingling between the venous and arterial blood. It is to be noted that the circulatory system of the fœtus contains fully oxygenated blood only in the umbilical vein which conveys the blood from the placenta of the mother towards the fœtal heart. This vessel divides into two branches, which unite with the inferior vena cava and the portal vein. Consequently, the placental blood loses its arterial character at some distance from the heart as soon as it is mixed with the venous blood returned from the posterior parts of the fœtal body. The aforesaid orifice closes as a rule very shortly after birth, but may also persist for a longer period of time. It need scarcely be mentioned that those infants in whom this orifice remains widely open, permitting an intermingling between the freshly aerated and non-aerated blood, cannot survive, because their tissues do not receive the required amounts of oxygen.

CHAPTER XIII

THE HEART OF THE MAMMALS

The Cardiac Cycle.—While the mammalian heart contains four separate chambers, it should be clearly understood that its two auricles contract together, and that their contraction precedes that of the ventricles by about one-tenth of a second. The contraction of the heart is known as *systole,* and its relaxation as *diastole.* The latter period is followed by a distinct phase of *rest.* A complete beat of this organ, beginning with the contraction of the auricles and ending with the pause of the ventricles, is commonly designated as a *cardiac cycle.*

Under normal circumstances, the heart of a man of medium size completes about 70 cycles in one minute, while that of woman beats 80 and that of children 90 times in a minute. Consequently, each cycle must consume about 0.8 of a second, half of this time being occupied by the pause. It will be seen, therefore, that the normal heart works as much as it rests. When, however, its frequency is greatly increased, its period of rest is materially shortened, so that an organ beating at the rate of about 140 times in a minute, would show only its successive systolic and diastolic movements without the intervening pauses. The heart reacts very promptly to changes in the outside temperature and temperature of the body. Muscular exercise increases its rate considerably, while rest and sleep decrease it to something like three-fourths its normal rate.

The General Arrangement of the Valves of the Heart.—The preceding discussion pertaining to the action of the simple tubular heart has brought out the important fact that the orderly flow of the blood is accomplished by two factors: namely, the successive contraction of the different portions of this organ, and the proper opening and closure

of its valves. The same conditions prevail in the hearts of the mammals. Each cardiac cycle is initiated by the practically simultaneous contraction of the auricles. Immediately upon the completion of the systole of these chambers, the ventricles begin their systolic movement. While this wave of activity sweeps over this organ the valves guarding its different orifices are shifted in such a way that the blood must flow from the auricles into the ventricles, and thence into the large arteries.

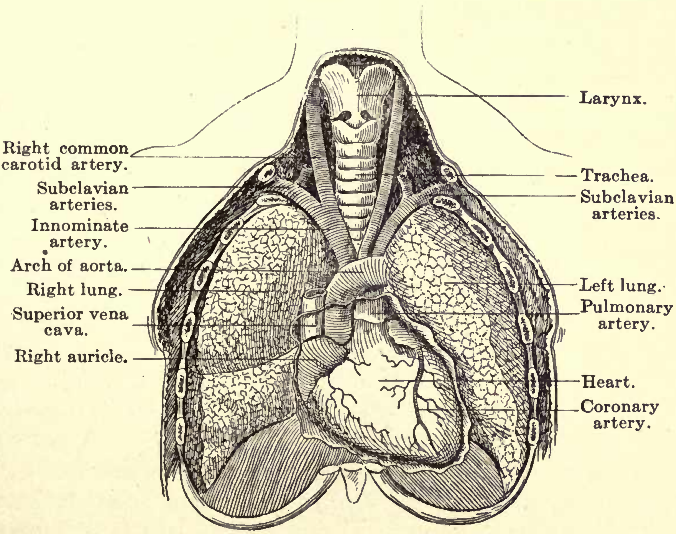


FIG. 56.—Relation of lungs to other thoracic organs. (*Ingals.*)

Having become acquainted with these general facts pertaining to the action of the heart, we are now in a better position to study the structure and arrangement of these valves in somewhat greater detail. It is to be noted first of all that the venous entrances to the heart are not guarded by valves, although the size of these openings may be somewhat diminished by the contraction of those muscle fibers which are arranged circularly around their lumina. These muscle cells act somewhat in the manner of the stop of a

photographic camera, although it has been shown that they do not obliterate these passages entirely. In fact, such a closure is quite unnecessary inasmuch as the systole of the auricles cannot produce a pressure high enough to reverse the venous bloodstream.

The remaining orifices of the heart are all guarded by valves. They are the left and right auriculo-ventricular

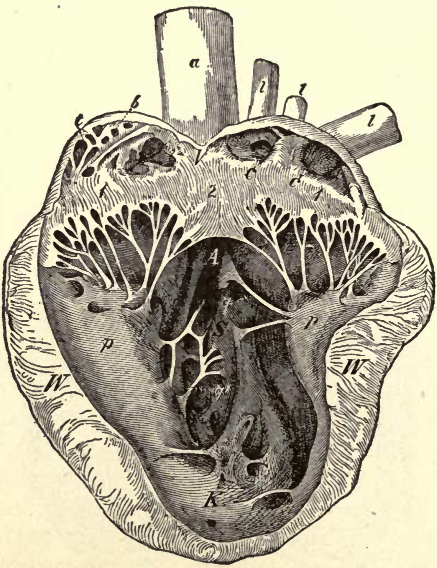


FIG. 57.—Heart of the cow, with left auricle and ventricle laid open. *a*, Root of the aorta; *b*, spaces in the wall of the auricle; *c*, *c*, orifices of the pulmonary veins; *l*, *l*, pulmonary veins; *p*, *p*, papillary muscles; *q*, *q*, columnæ carneæ. *A*, orifice of the aorta; *K*, left ventricle; *S*, septum; *V*, left auricle; *W*, lateral wall of left ventricle; 1, 1, 2, leaflets of mitral valve. (*Müller.*)

valves and the aortic and pulmonary valves. Accordingly, the valves of the heart may be arranged in two sets: namely, those guarding the communications between the auricles and ventricles, and those situated in the beginning portions of the aorta and pulmonary artery. The former are designated as the *mitral* and *tricuspid*, and the latter as the *aortic*

and *pulmonary semilunar valves.* The mitral valve consists of two large flaps, the basal portions of which are attached to the margins of the relatively large orifice on the left side, while the tricuspid embraces three flaps and is set in the somewhat triangular right orifice. Each semilunar valve embraces three cup-shaped flaps, their convex surfaces being turned toward the ventricles.

Intracardiac valves	auriculo-ventricular set	mitral (left)
		tricuspid (right)
	semilunar set	aortic
		pulmonary

Besides these intracardiac valves, the vascular system is also in possession of a large number of valves which guard the orifices of the smaller veins at their points of union with larger ones. These *venous valves* usually consist of two cup-shaped flaps which open only in the direction of the heart, and close immediately if the pressure in the more central vein rises above that prevailing in the tributary vessel.

The Action of the Cardiac Valves.—Inasmuch as the orifices between the auricles and ventricles are large, while those leading into the main arteries are relatively small, it need not surprise us to find that these valves present certain structural differences in accordance with their location. In the first place, it should be noted that the several segments of each valve are formed by simple duplications of the general lining membrane of the heart, known as the endocardium. But in order to give a greater stability to these flaps, a certain amount of fibrous tissue and a few elastic fibers have been added to their framework. As has just been stated, the bicuspid or mitral valve consists of two large flaps, whereas the tricuspid valve embraces three segments. This arrangement is in keeping with the general outline of these orifices, that on the left side being oval and that on the right side somewhat triangular.

While these valve flaps are surprisingly thin, they are nevertheless very strong, and cannot easily be torn with the fingers. Their basal zones are fastened to the walls of the orifice, while their tips are somewhat pointed and project

free into the lumen of the cavity. When a valve is completely closed, its different flaps assume a position transversely across the orifice and are firmly united with one another at their margins. Their thorough approximation is accomplished with the aid of threads of tendinous tissue, known as the *chordæ tendineæ.* When the cavity of either ventricle is opened, it will be noted that its surface is very uneven, and presents many prominent longitudinal strands

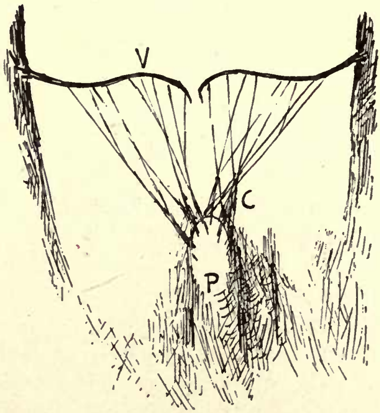


Fig. 58.—Schema to show fan-like distribution of chordæ tendineæ (*C*) from a single papillary muscle (*P*), situated underneath (*V*), two adjoining valve flaps.

of muscle tissue which are designated as columns of flesh or *columnæ carneæ.* Several of these columns extend only about half-way up the ventricular wall, and terminate at this level in the form of rounded prominences. These muscular projections are termed *papillary muscles.* A fact of greatest interest to us at this time is that these structures serve as points of attachments for the tendinous cords which extend from here in an upward direction to establish connections with the under surfaces of the different valve flaps. In their course through the ventricular cavity these cords divide and subdivide repeatedly into a delicate fan-shaped network. The chordæ tendineæ possess a definite length, which equals the distance between the papillary muscles and the

different valve flaps when in the position of closure. It is needless to state that their function is to hold the latter firmly in place, so that they cannot be diverted into the auricles. Consequently, they serve the same purpose as the guy-rope of the sail-beam which allows the sail to be deflected by the wind, holding it firmly in place as soon as it has reached its proper position.

Another very interesting structure found in the right ventricle of certain animals, is the so-called *moderator band.* This structure presents itself as a rather thick strand of tissue which is stretched transversely across the cavity from the interventricular septum to the outer wall. Obviously,

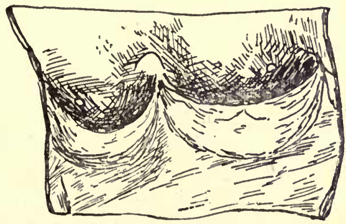


Fig. 59.—Longitudinal section through the root of the aorta showing cup-like shape of semilunar valve flaps.

the purpose of this cord is to hold the relatively thin wall of the right ventricle in place, so that it cannot be unduly distended. Inasmuch as the wall of the left cavity is very thick, it is not in need of a supporting structure of this kind.

The arterial orifices of the heart are comparatively small in size. Their walls are beset with three cup-shaped flaps, the concave surfaces of which are turned outward. No special mechanism in the form of tendinous cords is required to hold them in place, because their margins support one another when the valve is closed. During the phase of contraction of the ventricles, these flaps are turned outward, thereby allowing the blood to escape into the arteries. Contrariwise, the relaxation of the ventricles and consequent back pressure of the arterial blood cause their margins to snap together immediately. Being in this way prevented

from returning into the ventricles, the blood must follow the course of least resistance through the capillaries and veins.

In order to insure an orderly direction of the flow through the heart, the auriculo-ventricular and semilunar sets of valves must move in opposite directions to one another, but, naturally, their movements must remain the same on the two sides. It will be seen that the systole of the auricles deviates the auriculo-ventricular valve-flaps in a downward

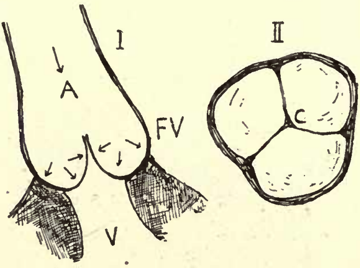


FIG. 60.—Diagram to show position of semilunar valve flaps on closure. *I*, longitudinal section; *II*, transverse section; *V*, ventricle; *A*, aorta; *FV*, fossa of Valsalva; *C*, corpora Arantii.

direction, *i.e.*, toward, but not against, the inner surfaces of the walls of the ventricles. During this period the contents of the auricles are quickly forced into the ventricular cavities. Scarcely has this act been completed when the ventricles begin their systolic phase. As the pressure within these chambers rises the auriculo-ventricular valve flaps are shifted into the position of closure, thereby preventing the blood from flowing into the auricles. The pressure in the ventricles now rises very rapidly until it finally exceeds that prevailing in the arteries. At this very moment, the flaps composing the semilunar valves are turned outward, thereby permitting the blood to escape into the arteries. Immediately upon the completion of the systole of the ventricles, the semilunar valves are closed, because at this time the arterial pressure exceeds that prevailing in the ventricles.

As soon as the auricles have completed their contraction, the high pressure existing in the veins causes the blood to enter their cavities. Finally, when a certain passive distention of their walls has been attained, the auriculo-ventricular valves open and allow a certain portion of the auricular blood to escape into the ventricles. Consequently, the auricular and ventricular cavities are already well filled

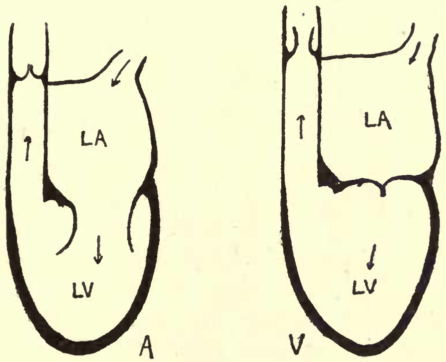


Fig. 61.—Diagram illustrating the position of the cardiac valves during (*A*) auricular systole and (*V*) ventricular systole. Only one-half of the heart is represented.

before the next systole of the auricles sets in. The contraction of the auricles, however, serves to fill the ventricles to their utmost capacity.

The Manner of Excitation of the Different Segments of the Heart.—When the action of the simple tubular heart is studied in detail, it will be noted that its contraction begins at the entrance of the large veins and spreads from here in the form of a wave to the adjoining auricles and ventricle. Consequently, this organ may be said to contract in a manner similar to that of the intestine, *i.e.*, peristaltically. It has been stated above that the mammalian heart does not possess a distinct sinus portion, but a closer observation will show immediately that its contractions also begin at the point of entrance of the venæ cavæ. This region embraces a small complex of tissue which is peculiarly receptive to

certain forms of stimuli and transfers the resultant waves of excitation to other areas of the auricles. Because of its power of initiating the heart beat, it is usually designated as the *pace-maker* of this organ.

The wave of excitation of the auricles is transferred to the ventricles over a bridge of specialized tissue which cannot be classified as nervous tissue, nor as muscle tissue. It is known as the *bundle of His*. The upper extremity of this connecting band of tissue is indicated by a nodular enlarge-

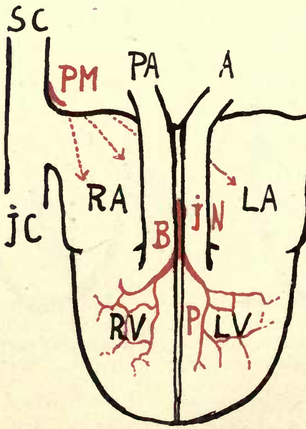


FIG. 62.—The conduction system of the heart. *SC*, superior vena cava; *IC*, inferior vena cava; *RA*, right auricle; *LA*, left auricle; *RV*, right ventricle; *LV*, left ventricle; *PA*, pulmonary artery; *A*, aorta; *PV*, pulmonary veins; *PM*, pace-maker; *IN*, interauricular node; *B*, bundle of His; *P*, fibers of Purkinje.

ment situated in the wall between the auricles. It is designated as the *interauricular node*. The main bundle divides below into two branches which finally connect with the musculature of the ventricles by an intricate network of delicate fibers, commonly called the *fibers of Purkinje*. It appears therefore, that the different portions of the heart are activated consecutively in consequence of an excitation developed in the pace-maker.

The substance of the heart is made up of three layers: namely, an internal lining membrane or *endocardium*, a

median coat of muscle tissue or *myocardium*, and an outer covering or *epicardium*. The outer limiting membrane is reflected from the large vessels at the base of this organ to form a pouch, the external wall of which is termed the *pericardium*. By this reflection a narrow space is cut off from the general cavity of the thorax which is called the *pericardial sac*. A small quantity of a lymph-like fluid is contained therein, which lubricates the inner surfaces of this sac, so that the heart may change its shape and position with the least possible friction and resistance.

The Sounds of the Heart.—The contraction of every muscle is attended by certain slight movements of its constituent fibers. In consequence of this displacement, an intercellular friction results which gives rise to a noise. When the mass of contracting muscle tissue is large, this noise may be perceived with the naked ear, while under less favorable conditions it becomes necessary to employ delicate amplifying devices. The heart does not form an exception to this rule, because the contraction of its musculature produces a very characteristic sound which is clearly audible and may be registered by means of micro-phonographic appliances. Even small excised segments of the ventricles yield a sound when they contract, but its audibility is correspondingly decreased.

It is a well known fact that the ear when applied to the region of the apex of a person's heart, perceives two distinct sounds during each cardiac cycle. These sounds may be transferred in almost their complete intensity by means of an instrument which is known as a *stethophone*. Their practical importance is based upon the fact that they betray to us not only the frequency of the heart, but also the manner of action of its different valves. It has been thoroughly established that any impairment in the opening or closure of their several valve-flaps gives rise to very characteristic changes in the quality of the normal sounds. These murmurs must be studied by the physician with the greatest care in order to be able to determine the character and location of the valvular lesion.

The first sound is heard during the period of contraction

of the ventricles, and possesses a rather low pitch and dull quality. The second sound is noted at the very beginning of the diastolic phase and presents a sharp, snappy character. Both sounds may be represented by the syllables "lūbb-dupp" or "tā-ta." More recently, a third sound has been discovered, which is quite inaudible in most persons, but may be perceived in all individuals by means of sensitive amplifying instruments.

The cause of the first sound lies in the contraction of the ventricular musculature, although it cannot be denied that its quality is slightly modified by the closure of the mitral and tricuspid valves. The cause of the second sound is wholly valvular, because no muscular activity occurs during diastole. The valvular change effected at this time is the closure of the semilunar valves. Hence, it may be concluded that the second heart sound is occasioned by the closure of the aortic and pulmonary valves.

The Apex Beat or Cardiac Impulse.—When the surface of the chest is inspected, it will be observed that the region of the apex of the heart bulges outward with every contraction of the ventricles. The area so affected measures about 2 cm. in diameter and is situated in men in the fifth intercostal space slightly below and to the right of the left nipple. In woman this protusion is more frequently observed in the fourth intercostal space. Its cause is to be sought in the impact of the systolic ventricles against the wall of the chest. To the physician the location and character of this impact betray changes in the size of the heart or of its several compartments as well as alterations in the strength of its beat.

Valvular Lesions of the Heart.—It need scarcely be emphasized that the improper closure of any one of the valves of the heart must lead to an impairment in the flow of the blood through its chambers and hence, also to disturbances in the peripheral circulation. The cardiac valves may become insufficient in their action for two reasons: Thus, the flaps may lose their soft, yielding texture in consequence of infiltrations, and cease to move freely upon their basal portions. Since their tips can then no longer be forced widely apart, the orifice guarded by them must be greatly diminished

in size. This condition which is known as *stenosis*, may also be occasioned by the partial growing together of the margins of the adjoining valve-flaps. Although usually inherited, this defect may also be acquired in the course of inflammations of the lining of the heart, designated as endocarditis.

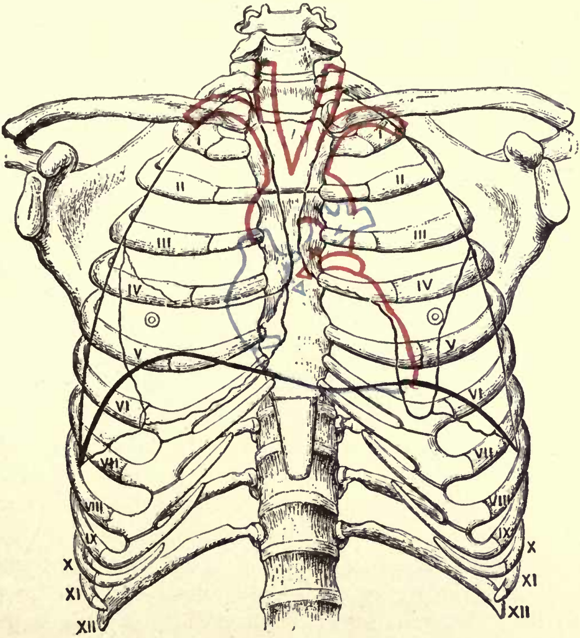


FIG. 63.—Showing location of apex beat. The positions of the aortic semilunar (+) and mitral (Δ) valves are indicated in red and those of the pulmonary semilunar (+) and tricuspid (Δ) in blue.

Secondly, the flaps cannot be made to close perfectly, because their margins are not fully approximated. A small opening is then left between them through which the blood escapes backward into the cavity from which it has just been ejected. This condition is known as *regurgitation*. Almost any valve may be the seat of a lesion of this kind, although the mitral is more frequently affected than the others. In

general, therefore, it may be said that a stenotic valve is altogether too unyielding, whereas a regurgitating valve is really too flexible. Thus, one of its chordæ may have been subjected to a strain with the result that the corresponding flap now assumes a position beyond that occupied by it during the normal closure of the orifice. In many instances, however, the flaps of a regurgitating valve show nodular growths upon their margins which prevent their perfect approximation.

When the musculature of any portion of the heart is forced to drive the blood through too narrow a valvular orifice, it gradually increases in size. This condition is known as *hypertrophy*. Obviously, this increase in its volume and pumping force enables it to sustain the circulation in spite of the aforesaid resistance to the flow. The same change follows regurgitating lesions, because if a portion of the blood is always returned into the cavity from which it has just been ejected, the musculature of this segment must do more work in order to be able to deliver a sufficient quantity of blood to the arteries. Very similar conditions prevail in a pump that possesses a leaky valve. We well know that we must pump much more forcefully and oftener at this time in order to collect the required amount of water.

A heart which overcomes the effects of these valvular lesions by hypertrophy and other means, such as an increase in its frequency of contraction, is said to be compensating and may last for many years, although constantly acting close to its functional limit. When a heart fails to hypertrophy or has reached its limit of endurance, owing to continued strain, it often *dilates* very abruptly, thereby putting an end to the circulation and life. A dilated organ is large in size, but its walls are relatively thin. This fact indicates that its muscular elements have been excessively distended and are no longer able to act even against the ordinary resistances of the vascular channels.

The Electrical Energy Liberated by the Beating Heart.—Attention has previously been called to the fact that living matter liberates three principal forms of energy: namely, mechanical energy, heat, and electricity. The heart

furnishes mechanical energy in the form of the pressure required to drive the blood through the vascular system. The heat evolved by it is measurable, but does not exceed that liberated by skeletal muscle. Lastly, its electrical energy may be detected by connecting the exposed heart of an animal with the poles of an electrical indicator, such as a string-galvanometer.

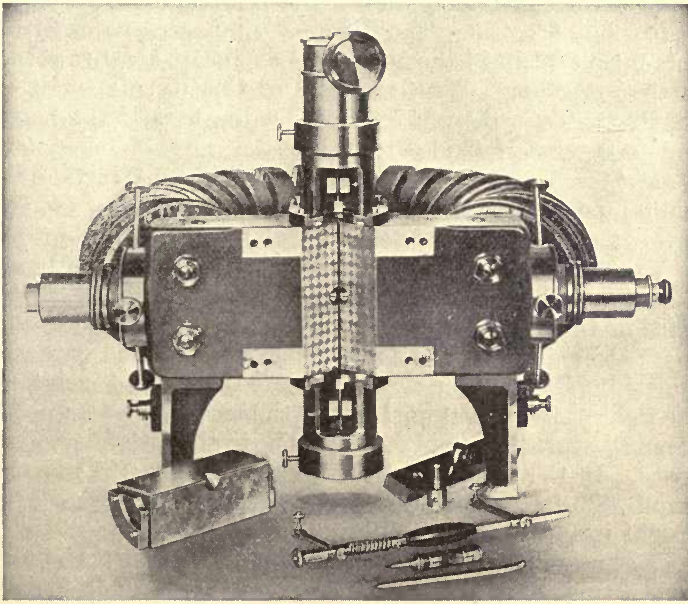


Fig. 64.—Einthoven's string galvanometer, as modified by H. B. Williams. The front-cover has been removed to show the position of the string between the poles of the magnet. The connecting posts lie behind the hood containing the string.

In very recent years, a method has been devised by means of which it is possible to observe and measure the electrical variations produced in the normal human body in consequence of the activity of the heart. The hands of the subject are placed in receptacles containing a solution of zinc sulphate. Each hand firmly grasps a platinum electrode which

is connected with the string-galvanometer by means of a copper wire. The galvanometer consists of a powerful magnet between the poles of which is suspended a fiber of quartz coated with silver. When the electrical differences produced in the body by the beat of the heart are allowed to act upon this magnet, the indicator is deflected in a very characteristic manner. These deflections may be observed by means of a microscope and may be projected into a camera to be photographed. The different appliances required to obtain this record of the activity of the heart constitute the *electrocardiograph*. With the help of this instrument it is possible to detect any irregularity in the beat of the heart and to obtain a fair idea regarding the cause of the latter.

The Size, Weight and Position of the Human Heart.—The adult human heart is lodged in the mediastinal space between the lungs, nearer the ventral than the dorsal wall of the chest. It is roughly triangular in shape, its basal portion being directed upward, backward and to the right, while its tip or apex is turned downward, forward and to the left. Consequently, the longitudinal axis of this organ is directed obliquely from a point situated about 1½ inches to the right of the mid-sternal line at the second rib, to a point about 3½ inches to the left of this line in the fifth intercostal space. In the adult male, the heart measures 125 mm. in length, 87 mm. in breadth, and 62 mm. in thickness. Its weight is approximately 310 grams and its volume 250 c.c. Its size may be said to equal that of the closed fist of the person to whom it belongs. The heart of the adult female weighs 250 grams.

CHAPTER XIV

THE FLOW OF THE BLOOD

The Circulatory System.—The greater and lesser circuits of the vascular system arise from the heart as single tubes, their repeated division and subdivision eventually giving rise to a large number of arteries, arterioles, and capillaries. For this reason, the arterial system has been likened to a tree, the trunk of which corresponds to the aorta, while its branches may be said to represent the smaller subdivisions of this supply tube. This comparison is a very appropriate one, although it does not represent the entire system. It leaves out of account the collecting channels which usually pursue a course parallel to the arteries. Inasmuch as the student is frequently at a loss to obtain a clear picture of the vascular systems from anatomical diagrams and descriptions, it seems advisable at this time to introduce a schema, such as is represented by Fig. 65, which deals with the many bloodvessels as if they were single tubes.

The greater or systemic circuit begins with the aorta. This vessel sends branches towards the head as well as towards the feet. In either case, the blood successively traverses certain arteries, arterioles, capillaries, venules, and veins, and finally returns to the right auricle and ventricle. After its ejection into the pulmonary artery it passes through the different vessels of the lesser or pulmonary circuit, and re-enters the heart at the left auricle. As has been stated above, the aorta supplies all the tissues and organs of the body, excepting the lungs. In the tissues the blood loses a portion of its oxygen and acquires carbon dioxid. The blood retains this character until it has been diverted into the capillaries of the lungs, where it discharges its carbon dioxid and acquires oxygen.

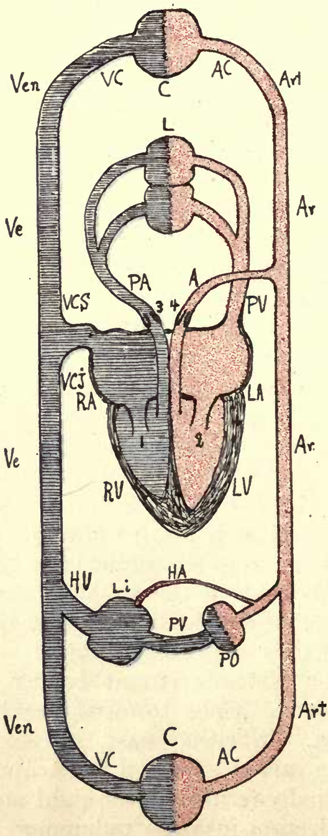


FIG. 65.—Schema of the circulation. *A*, aorta; *Ar*, arteries; *Art*, arterioles; *AC*, arterial capillaries; *C*, capillaries; *VC*, venous capillaries; *Ven*, venules; *Ve*, veins; *VCS*, vena cava superior; *VCJ*, vena cava inferior; *RA*, right auricle; *RV*, right ventricle; *LA*, left auricle; *LV*, left ventricle; 1, tricuspid valve; 2, mitral valve; 3, pulmonary semil. valve; 4, aortic semil. valve; *PA*, pulmonary artery; *L*, lungs; *PV*, pulmonary veins; *PO*, portal organs; *PV*, portal vein; *HA*, hepatic artery; *Li*, liver; *HV*, hepatic vein.

It should also be remembered that the systemic or greater circuit embraces two smaller divisions which exhibit certain details not presented by the others. The most striking de-

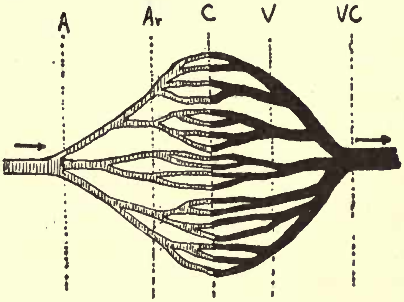


Fig. 66.—Diagram to illustrate the changes in the cross-section of the vascular system. *A*, aorta; *Ar*, arteries; *C*, capillaries; *V*, veins; *VC*, vena cava.

parture from the usual arrangement is made by the blood-vessels supplying the *portal organs*. The group of organs here referred to includes the stomach, intestine, pancreas, spleen, and liver. Each of these is supplied with arterial

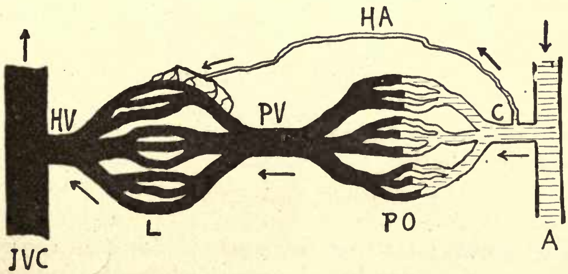


Fig. 67.—Schematic representation of the portal circuit. *A*, abdominal aorta; *C*, cœliac axis supplying portal organs; *HA*, hepatic artery supplying the frame work of the liver. *PO*, portal organs (stomach, intestines, spleen, and pancreas); *PV*, portal vein; *L*, liver; *HV*, hepatic veins; *IVC*, inferior vena cava.

blood which is derived from the cœliac and mesenteric branches of the abdominal division of the aorta. Their venous drainage, however, is not collected by separate channels but by a single one, which is called the *portal vein*.

In the liver this vein divides into many smaller branches which in turn give rise to an intricate network of capillaries. Centrally to this organ, the hepatic veins convey this blood into the inferior cava. This arrangement allows the cells of the liver to make first use of the nutritive material which has traversed the lining of the alimentary canal before it is permitted to enter the general circulation. The substances here worked over are the simple sugars and amino-acids.

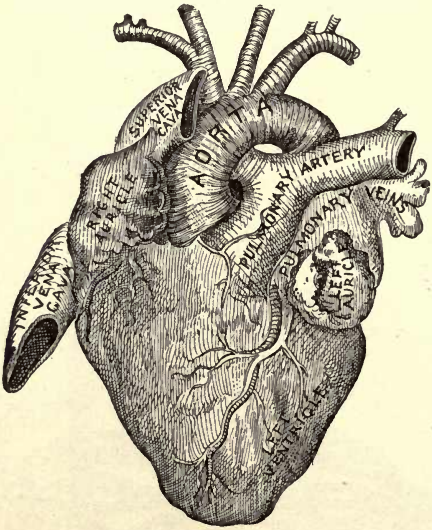


Fig. 68.—The heart. (*Stoney.*)

It will be shown later that the sugar is stored in the cells of the liver in the form of glycogen, while the amino-acids are employed in the production of urea, an important constituent of urine.

The bloodvessels of the heart form an exception to the general arrangement only insofar as they arise from the root of the aorta and connect directly with the right auricle. This circuit which is set aside for the nutrition of the substance of this organ, is known as the *coronary*. It begins as a rule with two arteries, the orifices of which lie behind the

semilunar flaps, and forms a superficial as well as a deep set of smaller vessels. The coronary veins eventually unite into a single channel which is known as the *coronary sinus.* It empties directly into the right auricle.

It will be seen, therefore, that the contents of the aorta are diverted into a very large number of vessels. Possibly the shortest route that may be selected by the blood in its return journey to the right auricle, is the coronary circuit. A much longer time is required for its passage through the portal organs, kidneys, and extremities.

The Structure of the Bloodvessels.—The walls of the arteries are made up of three layers of tissue: namely, an inner lining of epithelium or intima, a middle coat of smooth muscle cells intermingled with connective tissue, and an outer layer of connective tissue. By far the largest number of muscle cells are arranged circularly around the lumen of the vessel. They are particularly numerous in the arterioles, while in the central arteries the elastic connective tissue is present in preponderating amounts. Accordingly, it may be surmised that the aorta serves the purpose of an elastic reservoir, while the peripheral vessels possess the power of influencing the bloodstream in an active manner by lessening the size of the channel.

The capillaries possess very thin walls which are composed of plate-like endothelial cells cemented together at their edges by intercellular substance. Each cell is equipped with a small oval nucleus. The diameter of these tubules varies considerably, some of them being so small that the red corpuscles cannot enter them without being considerably elongated. Others, again, permit two or three of these elements to pass side by side. Consequently, it may be said that their average diameter is something like 15μ or $\frac{1}{2000}$ of an inch. Their average length is 1 mm. They appear as small-meshed networks, in the interspaces of which lie the individual tissue cells. It should be noted, however, that some tissues are not in possession of capillary systems of this kind, and are nourished solely by lymph. In this group of tissues belong the nails, hairs, outer layer of the skin, and central area of the cornea of the eye. It will easily be seen

that bloodvessels would seriously impair the passage of the rays of light into the interior of the eye.

The walls of the veins are much thinner than those of the arteries. This structural difference is due to the fact that they contain a very small amount of muscle tissue and elastic fibers, but a large amount of ordinary connective tissue. On this account, the caliber of the veins may be made to fluctuate considerably in accordance with the changes in internal pressure. Their walls collapse very readily when this pressure is withdrawn.

It is also of interest to note that the venous channels are equipped with many valves which are usually placed at the points where the smaller veins unite with larger ones. In perfect agreement with the structure of the lymphatic valves, these structures are composed of two hemispherical membranous cups, the margins of which are brought together immediately if the central pressure surpasses that prevailing in the more distal vessel. These valvular mechanisms effectively oppose the backward displacement of the column of blood whenever the vein is compressed by an external force. Thus, every contraction of the muscles must tend to propel the venous blood in the direction of the heart and not toward the periphery. Inasmuch as the superficial veins of the arms and legs are more directly exposed to these impacts than the deeper ones, they are equipped with an especially large number of these valves.

The position of the venous valves in the hand and forearm may easily be determined in the following manner: To begin with, the subject should hold his arm for a few moments in a dependent position, so as to fill the veins well with blood. A piece of soft rubber tubing is then lightly wound around the arm near the elbow. On raising the arm to about the level of the heart, the veins will be sharply outlined against the integument. If one of the smaller veins is now compressed with the tip of the index finger of your right hand, while its contents are squeezed into the next collecting channel by drawing the index finger of your left hand gently across this vein in a direction from periphery to center, the point of entrance of the tributary vein will be clearly marked off by a

rounded eminence. Obviously, the closure of the valve situated at the confluence of these veins, does not permit the blood to re-enter the more peripheral segment.

The Flow of the Blood.—The chief purpose of the circulation is to supply the different tissues with nutritive material and to remove from them their waste products. This interchange is accomplished in the capillaries, where the blood and lymph are separated from one another by only a thin layer of plate-like cells. When considered from the stand-

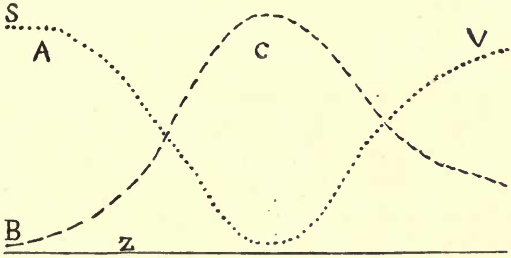


FIG. 69.—Diagram to illustrate the relationship between the size of the blood-bed and the velocity of the flow. *B*, cross-section; *S*, speed of flow in (*A*) arteries; *C*, capillaries and (*V*) veins; *Z*, zero line.

point of metabolism, the arteries and veins are of lesser importance than the capillaries, because they merely play the part of supply and drainage channels for the latter. It cannot surprise us, therefore, to find that the arterial bloodflow is very rapid, while that in the capillaries is surprisingly slow. Obviously, since the aforesaid interchanges take place in the tissues, a sufficient time must be allowed the blood in which to unload its nutritive substances and to acquire the tissue waste. In the arteries and veins, on the other hand, the speed of the blood may well be much increased, because practically no cellular interchanges are accomplished here.

It has been shown by means of various instruments, that the speed of the bloodflow is greatest in the arteries, least in the capillaries, and intermediate in the veins. Such arteries as the common carotids which supply the region of the head, are traversed with a velocity of about 250 mm. in a second.

Accordingly, it might be conjectured that the blood traverses the body of a person of average height in the course of about 6 to 8 seconds. It has been stated, however, that the speed of the blood is markedly diminished by the friction encountered by it during its passage through the capillaries and hence, a very much longer time must be required for its complete circulation. The value usually given is 30 seconds,

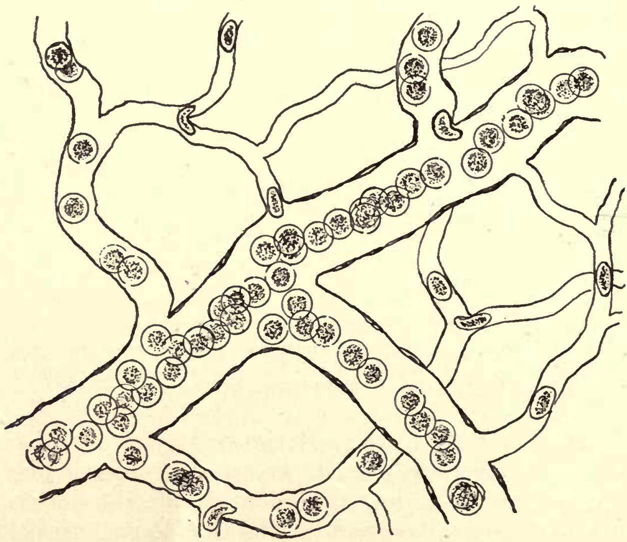


FIG. 70.—Area of capillaries. Tubules of different diameter are shown, some so small that the red cells cannot enter at all and others through which they can only pass by assuming an elliptical outline.

so that about 35 heart beats are necessary in order to drive a droplet of blood from the left ventricle to the right auricle.

The average velocity of the bloodflow in the capillaries is something like 1.0 mm. in a second, and that in the veins about 60 mm. in a second. In explaining this sudden reduction in the speed of the flow at the capillaries, brief reference should first be made to the fact that the speed of flow of a river is always greatest at the point where the cross-section of the river-bed is smallest. Repeated measurements have proven that the lumen of an artery is always very

much smaller than the cross-area of the corresponding system of capillaries. Thus, it may be concluded that the cross-section of all the arteries combined is considerably smaller than that of all the capillaries. Consequently, the velocity of the bloodflow must be correspondingly greater in the arteries, because the quantity of the circulating blood does not change materially from moment to moment. The veins occupy an intermediary position in size as well as in the speed with which the blood traverses them.

The circulation of the blood may be observed directly by placing certain translucent tissues under the ocular of a microscope. The preparations usually made use of for this study are the web and mesentery of the frog. Our attention is first attracted by the amazingly large number of tubules of different caliber which one of these small microscopic fields presents. Through some of these the blood rushes with such great speed that its corpuscular constituents cannot be made out at all, while others contain only a few slowly moving red cells at considerable distances from one another. In reality, of course, the bloodflow is not so rapid, because the ocular subjects the preparation to a magnification of possibly fifteen diameters. Undoubtedly, the most interesting picture is presented by those capillaries which possess a diameter somewhat smaller than that of the red cells, so that these elements cannot get through them unless considerably compressed from side to side. When observing the places of bifurcation of some of these capillaries, one may note how the red cells are thrown against the sharp edge between them, and are rocked back and forth a number of times before they actually succeed in escaping into one or the other of the distal branches. The arterioles are easily recognized, because they are larger in size and possess relatively thick walls. The blood traverses them with a speed considerably greater than that observed in the capillaries proper. Contrariwise, the venules possess thin walls, and contain blood somewhat darker in color than that of the arterioles. The speed of the blood flow in the venules is considerable, although not quite so rapid as that noted in the arterioles.

CHAPTER XV

BLOODPRESSURE AND RELATED PHENOMENA

The Differences in Pressure.—It is a well known fact that if the outer layer of the skin is scraped off, a large number of bleeding points will appear, indicating the locations of the opened vessels. The small drops of blood oozing out of them, finally coalesce and cover the injured region with a thin coagulum. If, however, the part is incised more deeply, the blood rushes forth in much greater volume, its manner of escape becoming jet-like when a larger artery has been cut. While an opened vein also sends forth a large amount of blood, the force with which it is ejected is by no means considerable. These simple facts prove very clearly that the blood is held in the vascular system under a certain pressure, commonly designated as *bloodpressure*. This pressure is greatest in the arteries, intermediate in the capillaries, and least in the veins. Obviously, therefore, the circulation of the blood depends upon the same factors as the flow of water. It is driven through a series of tubes, meanwhile constantly endeavoring to escape from the high pressure to which it has been subjected by the action of the heart. The pressure originally imparted to it by this organ, is gradually used up in consequence of the resistance resident in the vascular channels.

The term bloodpressure is usually employed to designate the pressure existing in the large arteries. This pressure is actually somewhat lower than that prevailing in the left ventricle, but very much higher than that existing in the capillaries and veins. Supposing that the left ventricle develops a pressure of 120 mm. Hg, we may expect the pressure in the aorta to be something like 115 mm. Hg, and that in the distal arteries, such as the radial at the wrist, about 100 mm. Hg. The fact that the pressure in two so

widely separated arteries shows only a relatively slight difference, clearly proves that the resistance encountered by the blood in the arterial system is inconsiderable. Hence, only a comparatively small portion of the original pressure is lost in driving the blood as far as the arterio-capillary junction. Very different conditions are met with in the capillaries. Because of the enormously increased friction, these tubules must give rise to a very decisive fall in pressure or "loss in head," as the hydraulic engineer would call it. Accurate measurements have demonstrated that the pressure in the true capillaries amounts to only about 40 mm.

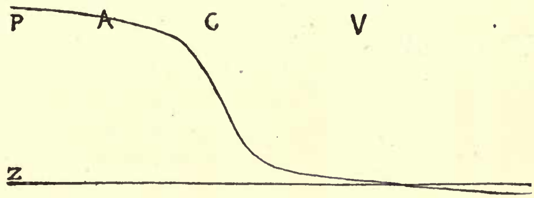


FIG. 71.—Diagram showing changes in pressure in the vascular system. *Z*, abscissa or zero-line; *P*, curve of pressure (*A*) in arteries (*C*) in capillaries and (*V*) in veins. The greatest fall in pressure occurs in the capillaries in which the resistance is greatest.

It will be seen, therefore, that the driving force imparted to the blood by the action of the heart, is spent very largely in overcoming the resistance resident in these fine tubules. This conclusion is substantiated by the fact that the pressure in the distal veins equals only about 10 mm. Hg. It becomes apparent immediately that this pressure is entirely inadequate to force the blood into the right auricle, the distance still to be covered amounting in many instances to one meter and more. This difficulty is overcome by the fact that the distended lung tissue exerts a constant pull upon the outer surfaces of the soft and yielding walls of the central veins, establishing therein a pressure somewhat below the atmospheric. Actual measurements of the pressure prevailing in the veins near the right auricle, have yielded a value of -5 to -10 mm. Hg. Accordingly, it may be said that the blood enters the greater or systemic circuit under a pressure of about 120 mm. Hg and leaves it under a pressure of about -5 mm.

Hg. The greatest loss in pressure takes place in the capillaries. Very similar conditions prevail in the lesser or pulmonary circuit, although these pressures are much lower throughout. Entirely in accord with the work demanded of it, the right ventricle produces a systolic pressure of only about 40 mm. Hg.

Methods of Determining the Bloodpressure.—In order to determine the height of any pressure, it becomes necessary to oppose and balance this pressure by a force of known magnitude. We employ for this purpose as a rule a column of mercury which is retained in a U-shaped tube of glass. This instrument which is known as a *manometer*, is connected by means of rubber tubing with the artery in which the pressure is to be ascertained (Fig. 72 *M*). The connecting tube

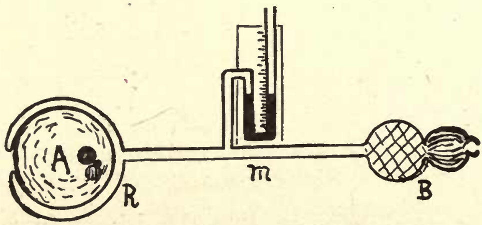


Fig. 72.—Diagram illustrating the indirect method of measuring bloodpressure. *A*, arm surrounded by a flat rubber pouch, *R*; by means of a rubber bulb, *B*, a pressure is set up in this system of tubing sufficient to compress the artery. This moment is indicated by the manometer (*M*).

is filled with a solution of sodium carbonate to keep the blood from coagulating. As soon as the clip has been removed from the artery, the blood enters the tubing and displaces the mercury outward until the latter has accurately balanced the pressure. The degree of displacement of the mercury, *i.e.*, the height to which it rises, serves as the index of the internal pressure. But since the tube is U-shaped, the level of the mercury must fall in its central limb and rise an equal distance in its distal limb. Consequently, the height indicated by the recording needle of the manometer must be multiplied by two. The standard of measurement is the millimeter.

The procedure here briefly outlined constitutes the *direct* method of registering the bloodpressure. It is applicable only to animals. Upon human beings we make use of the *indirect* method, the principle of which is to exert a known outside force upon a bloodvessel until its lumen has been completely obliterated. It may rightly be concluded that the occlusion of the vessel must take place at the very moment when the external pressure just barely overcomes the internal pressure. Such an instrument invariably consists of three parts: namely, a narrow pouch of rubber, a pump for the inflation of the pouch, and a manometer for the registration of the pressure existing in this system. The artery usually selected for these tests, is the brachial. The pressure required to accomplish its compression, may be measured with the aid of either an ordinary mercury-manometer or a tension spring, such as is used upon boilers to register the steam-pressure. The former type of instrument is designated as a *sphygmomanometer* and the latter, as a *sphygmotonometer* (Fig. 73).

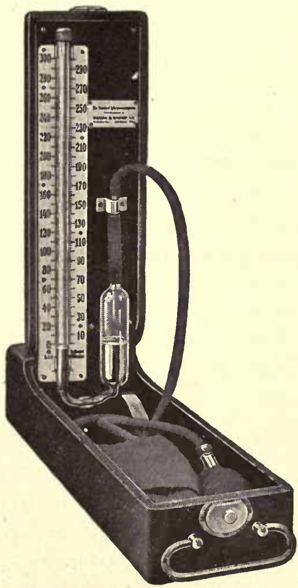


FIG. 73.—Sphygmomanometer of recent construction (manufactured by Green and Bauer).

The principle underlying the indirect method of ascertaining the bloodpressure, finds its origin in the practice of determining the arterial tension by palpation of the radial artery. Two or three fingers are usually used for this purpose, the aforesaid artery being compressed with the more central finger until the pulsations can no longer be felt by the more distal one. The force which is required to obliterate the pulse, serves as a subjective measure of the pressure prevailing within this vessel and the arterial system in general.

Palpation.—In ascertaining the bloodpressure by means of the sphygmomanometer, the rubber cuff takes the place of the central finger. It is usually applied to the arm, and is gradually inflated until the pulse at the wrist disappears. At the very moment of its disappearance the pressure in the arm-piece must have just overcome the pressure within the brachial artery. The value of the latter is indicated by the height of the column of mercury. This procedure may also be reversed in the following manner: Knowing that the bloodpressure of a normal person does not exceed 140 mm. Hg, the cuff is inflated to a point somewhat above this value. Naturally, the radial pulse is obliterated at this time. If the air is now allowed to escape slowly through the detention-ing valve, a point will eventually be reached when the radial pulse again becomes palpable. This point indicates the moment when the systolic arterial pressure just barely overcomes the outside pressure. A reading of the pressure is taken at this time.

Auscultation.—It will be shown later that the bloodpressure presents definite variations with every contraction of the heart, and every respiratory movement. Concerning the former, it should be noted at this time that the ejection of the ventricular contents raises the arterial pressure very abruptly to a point about 35 to 40 mm. Hg above that prevailing during the diastolic period of the heart. In other words, the arterial bloodpressure exhibits a systolic maximal and a diastolic minimal value with every cardiac cycle. The difference between these two values is designated as the *pulse-pressure.* Thus, supposing that the systolic pressure is 120 mm. Hg and the diastolic 80 mm. Hg, the pulse-pressure amounts to 40 mm. Hg.

While the procedure of palpation does not permit us to ascertain anything more than the systolic pressure, all of the aforesaid values may be obtained by the method of ausculta-tion. It is a well known fact that the compression of a blood-vessel gives rise to a noise distally to the point of constriction which is due to the formation of whirls in the distorted column of blood. Supposing then that the cuff is first inflated beyond the bloodpressure and is then gradually deflated, a

point will be reached when the systolic pressure breaking through the constricted area produces a sound which, as experience has shown, is best heard at the bifurcation of the brachial artery near the elbow joint. Accordingly, if a stethophone is applied to the ventral surface of this area at a distance of a few centimeters below the edge of the arm-piece, the systolic pressure will be indicated by very faint sounds comparable in a measure to those heard over the apex of the heart. If the cuff is deflated further, these sounds gradually increase in their intensity and suddenly disappear at a point about 40 mm. Hg below the systolic value of the pressure. At the very moment of their disappearance the manometer registers the diastolic pressure. Hence, supposing that these sounds first become audible at 120 mm. Hg, and disappear at 80 mm. Hg, the pulse-pressure amounts to 40 mm. Hg.

It should also be observed that the mercury in the tube of the manometer exhibits certain oscillations during the deflation of the cuff which may be used as a guide in detecting the points of maximal and minimal pressure. Although small at first, these fluctuations gradually increase in amplitude until the diastolic minimum has been reached.

The Height of the Arterial Pressure.—Inasmuch as the ventricular pressure is the basis of the circulation of the blood, and inasmuch as the life of the tissue cells depends upon a proper supply of blood, these measurements must necessarily play a very important part in ascertaining the functional capacity of the body as a whole. Experience has shown that the normal bloodpressure in men is about 120 mm. Hg and in women about 110 mm. Hg. Individual variations, however, are not uncommon, although it may be said that the upper normal limit for men is 140 mm. Hg and for women 130 mm. Hg. Pressures higher than these invariably suggest some abnormal circulatory condition. It is to be remembered, however, that the pressure increases constantly with age, owing chiefly to a diminution in the elasticity of the vessels. Thus, a pressure of 140 mm. Hg at 40 years of age is not uncommon, nor is one of 160 mm. Hg

at sixty years of age. The upper normal limit at this time of life is 180 mm. Hg.

It is true, however, that temporary rises and falls may be produced by various physiological means. Chief among these is *muscular exercise.* Thus, it is a matter of common experience that even slight muscular activity increases the frequency of the heart and causes the arterial pressure to rise 20 to 30 mm. Hg. Muscular exercise intensifies the circulation, because a larger quantity of blood must then be supplied to the working organs in order to cover more fully their requirement in nutritive material and to remove from them the extra amounts of waste. This increase in their metabolism accounts also for the greater respiratory activity invariably associated with muscular efforts. But these effects are only temporary in their nature, and normal conditions of pressure and flow are again established within a short time after the exercise, provided it has not been severe nor unduly prolonged. In the latter case, the pressure may retain a value somewhat below normal for some time.

Posture affects the arterial pressure in a very characteristic manner. As a rule, the change from the recumbent to the standing position leads to an increase in the rate of the heart which enables the bloodpressure to retain its normal value or to assume a level somewhat above normal. A marked fall invariably indicates a loss of tonus of the bloodvessels, allowing the influence of gravity to come into play. It is a matter of common experience that bodily and mental fatigue, as well as engorgements of the digestive organs, give rise to a series of peculiar symptoms, such as dizziness, unsteadiness, and general weakness. The reason for this must be sought in a deficient bloodsupply of the brain, brought about by the relaxation of the bloodvessels in other parts of the body. The vessels chiefly concerned in the production of these phenomena are those of the portal organs. Very similar reactions are often noted in persons who have been confined in bed for some time. Their bloodvessels must first regain their normal tonicity before they will be able to resist the effects of gravity.

Inasmuch as the metabolism of all the tissues is greatly diminished during *sleep*, it need not surprise us to find that the frequency of the heart, as well as that of respiration, retains during this period a value only about three-fourths of normal. For the same reason, the bloodpressure assumes at this time a level considerably below its usual one. These effects have been made use of repeatedly in explaining the phenomenon of sleep, it being held that the cells composing the higher centers enter this state of depressed function in consequence of a diminution in their bloodsupply. Thus, it is believed that the volume of the brain decreases during sleep, because a portion of the blood ordinarily allotted to this organ is temporarily diverted into the portal and cutaneous circuits.

A similar compensation takes place after *meals*. Inasmuch as a large amount of blood is then needed by the digestive organs, the general circulatory channels, inclusive of those of the brain, transfer a portion of their blood to the portal organs. Consequently, mental and bodily rest are to be recommended for some time after the ingestion of a meal in order not to impair the intensity of the digestive processes. Much, however, depends upon the quantity and quality of the food consumed. Excessive amounts of food frequently augment the general bloodpressure considerably. For this reason, persons whose bloodvessels have been rendered inelastic by calcareous infiltration, are at this time in particular danger of suffering a rupture of one of these brittle tubules.

Variations in the outside *temperature*, such as may be produced by cold and warm baths, give rise to very striking changes in the bloodpressure and flow. Since cold constricts the superficial vessels, their contents are temporarily diverted into the internal organs. Warmth applied to the body-surface, dilates these vessels and allows the blood to enter the external channels. The most efficient results are obtained by bathing in water of about 34° C., because this temperature constricts the cutaneous vessels and augments the force of the heart beats, thereby intensifying the entire circulation. Hot baths increase the frequency of the heart,

but dilate the vessels in such a measure that the circulation cannot be augmented.

Several of the aforesaid changes have been made use of in the compilation of certain tests by means of which the physical condition of a person may be rated. The most promising of these are those devised by Foster, Barrach, Crampton, Barringer, and Schneider.[1]

The Arterial Pulse.—If the finger is placed upon a superficial artery, such as the radial, an intermittent impulse will be felt which is due to the sudden distention and subse-

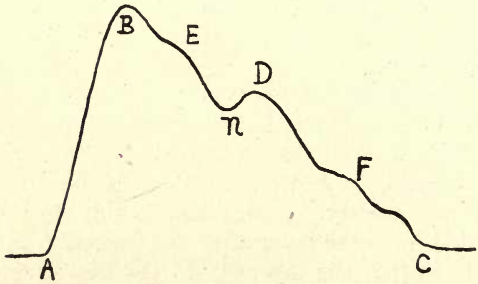


Fig. 74.—The character of the arterial pulse. *AB*, anacrotic limb; *BC*, catacrotic limb; *B*, apex; *D*, dicrotic wave; *N*, dicrotic notch; *E*, predicrotic wave; *F*, postdicrotic waves.

quent recession of the arterial wall. It need scarcely be mentioned that these pulsations originate in changes in the arterial pressure. The high systolic pressure forces the wall outward, while the diastolic pressure permits it to recoil. Consequently, it may be concluded that the cause of the pulse lies in the wave of high pressure produced in the arch of the aorta by the ejection of the ventricular contents. From here this wave advances rapidly through the smaller arteries until it is neutralized by the high resistance resident in the capillaries.

[1] See: Jour Am. Med. Assoc., 1914, lxii, 525 (Barrach); Med. News, 1905, lxxxvii, 529 (Crampton); Arch. Int. Med., 1915, xvi, 795 (Barringer); Jour. Am. Med. Assoc., 1920, lxxiv, 1507, and ibid., 1921, lxxvi, 705 (Scott).

The foregoing discussion must lead us to surmise that the pulsations in such arteries as the radial, carotid, and temporal, occur at clearly recognizable intervals after the corresponding systoles of the ventricle. This assumption may be proved to be correct by the simultaneous palpation of the wall of the chest in the region of the cardiac apex and of any one of the aforesaid bloodvessels. Furthermore, by applying two levers to a bloodvessel at a considerable distance from one another, it can easily be shown that the more distal lever is

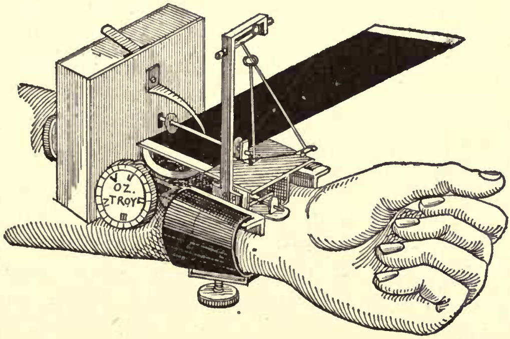


FIG. 75.—The Dudgeon sphygmograph in position.

moved at an appreciable interval after the central one. By comparing the distance with the time, it has been shown that this wave progresses with a velocity of 7 m. in a second. Hence, its speed is considerably greater than that of the arterial bloodstream which, as has been stated above, amounts to only 25 cm. in a second. In order to be able to recognize these two factors separately, the student is reminded of the fact that a stone thrown into a river produces ripples upon its surface which rapidly spread in all directions from the center of the disturbance. The speed with which these undulations advance is very much greater than that of the flow of the water.

The character of the arterial pulse is usually studied with the aid of an instrument which is known as a *sphygmograph*. Its principal part is a tension spring which is applied to the

region of the artery and communicates its displacements to a writing lever. As may be surmised, a record of any one of these pulse-waves exhibits two principal phases: namely, an upstroke corresponding to the distention of the vessel, and a downstroke indicating the subsequent recoil of its wall. It should be noted, however, that the downstroke is interrupted by a rather prominent elevation which is known as the *dicrotic wavelet.*

Obviously, inasmuch as the arterial pulse serves as an indication of the frequency of the heart, it is constantly employed by physicians in order to obtain an idea regarding the functional capacity of this organ. Accordingly, the pulse may be characterized as *rapid or slow,* and further more, if note is made of its quality, the experienced person may draw definite conclusions regarding the tension prevailing in the arterial system. Thus, the pulse is said to be *soft* when the pressure is relatively low and the vessels possess a proper degree of elasticity. A *hard* pulse, on the other hand, indicates a high bloodpressure and relative inelasticity of the vessels. The pulse is also described as *small* or *large,* these terms referring more particularly to its volume or magnitude.

In this connection brief reference should also be made to the fact that the central veins pulsate synchronously with the heart beat. The cause of this *venous pulse* lies in the fact that the changes in pressure occurring in the auricles, are propagated outward into the veins. It has been stated above that the venous orifices of the heart are not guarded by valves and allow a free communication with the veins even during the contraction of the auricles. A very convenient region for observing these pulsations is the jugular fossa, in the depth of which is embedded the central portion of the external jugular vein.

CHAPTER XVI

THE NERVOUS CONTROL OF THE HEART AND BLOODVESSELS

A. THE REGULATION OF THE BEAT OF THE HEART

The Excised Heart.—It is a well known fact that the heart may continue its activity even after it has been isolated from the central nervous system by severing all of its nerves. In fact, the excised heart of the lower animals will beat rhythmically for many days and even weeks if placed in a dish under favorable conditions of moisture and temperature. Very similar results may be obtained with the hearts of the mammals, but since these organs possess a smaller storative power, they must be supplied with a nutritive solution of some kind in order to enable them to continue their activity outside the body. Lastly, it is possible to excise small strips of the ventricle and to activate these preparations by immersing them in solutions of certain salts, for example, those of the chlorids of sodium, calcium, and potassium. Under favorable conditions these pieces of cardiac muscle will continue to beat rhythmically for many hours and even for days.

These facts clearly prove that the activity of the heart is not dependent upon the central nervous system, and that the stimulus to contract is brought to bear directly upon the tissues composing this organ. In this regard, cardiac muscle tissue differs materially from skeletal muscle, because every contraction of the latter is instigated by impulses from the higher nerve centers. Accordingly, it may be concluded that the central nervous system merely serves the purpose of correlating the automatic action of the heart with those of other tissues and organs. It is also a matter of common experience that the activity of this central pumping mechan-

ism may be markedly altered at any time by stimuli arising in other parts of the body, *i.e.*, in a reflex manner. The results that may be obtained in this way, are either a quickening or a slowing of its beat. The former effect is termed *cardio-acceleration* and the latter, *cardio-inhibition*.

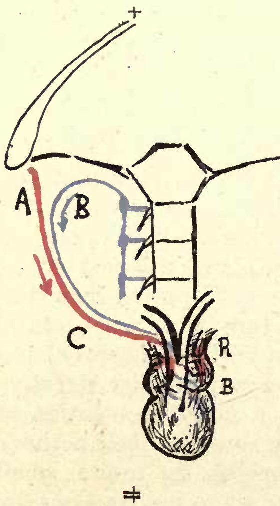


FIG. 76.—Schema to show the course of the cardiac nerves in the frog. *A*, vagal fibers are still separate; *B*, sympathetic fibers are still separate; *C*, both types of fibers have combined to form the vagosympathetic nerve. *R*, Remak's ganglion; *B*, Bidder's ganglion.

The Cardiac Nerves.—Having established this important fact, let us endeavor to trace the nervous connections by means of which the aforesaid impulses from the central nervous system are conveyed to the heart. Possibly the simplest anatomical relationship exists in the frog. We find here that the heart receives two sets of nerve fibers, one being derived from the vagi nerves, constituting the tenth pair of cranial nerves, and one from the sympathetic ganglia situated along the thoracic division of the spinal cord. It is entirely probable that both sets of fibers originate in certain nerve cells which occupy a part of the enlarged upper portion of the spinal cord or medulla oblongata. This group of cells forms the so-called *cardiac center*. It communicates with different afferent channels through which other parts of the body are enabled to influence its activity. In this manner its motor action may be varied in favor of either cardio-acceleration or cardio-inhibition. The nature of the impulses received determines the character of the reaction that is required by the other organs to conform to their state of activity.

The efferent impulses discharged by the cardiac center reach the heart by way of two separate channels. Those intended to slow its beat descend through the vagi nerves,

and those purposing to increase its frequency through the spinal cord and sympathetic system of the thorax. Near the heart these motor fibers ramify extensively to form a plexus, whence they are distributed to the pace-maker and ganglia within this organ. This arrangement is also clearly in evidence in the mammals, although anatomically more difficult to trace than in the amphibians and reptiles.

Inhibition of the Heart.—If the apex of the heart of a recently-killed frog is connected by means of a thread with a writing lever, properly arranged to register its excursions upon the paper of a kymograph, a record will be obtained such as is represented in Fig. 77. Provided the suspension

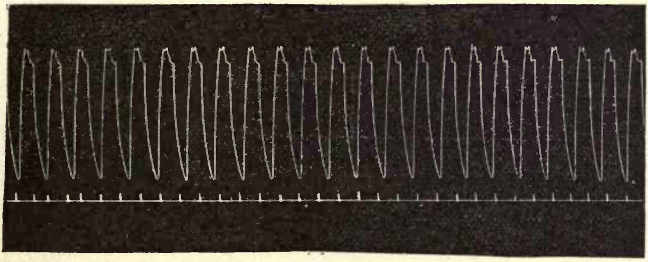


Fig. 77.—Record of the contractions of the frog's heart. The time is registered in seconds.

method is employed, the upstrokes of the lever indicate the systolic phases of the ventricle, and the downstrokes its diastolic periods. Various procedures may at this time be followed in order to determine their influence upon the action of the heart. A very simple experiment is to allow a few drops of warm or cold saline solution to flow over its surface. It will be noted that warmth increases the frequency of its beat, while cold diminishes it. Likewise, we may then isolate and stimulate the aforesaid motor nerves in an attempt to analyze their action in greater detail. When graphically portrayed in this way, the excitation of the vagus with a moderately strong current usually yields a record such as is represented in Fig. 78.

It will then be observed that the heart ceases to beat a few moments after the application of the current, its inhibi-

tion being indicated in the record by the straight line. Furthermore, as the heart becomes more and more diastolic, it gradually acquires a larger amount of blood. Complete inhibition, of course, means a highly distended organ and cessation of the circulation. The arterioles empty themselves slowly by transferring their contents into the larger veins. This condition is practically identical with that established shortly after death, when the recoil of the arterial walls drives the blood into the central veins and right side of the heart.

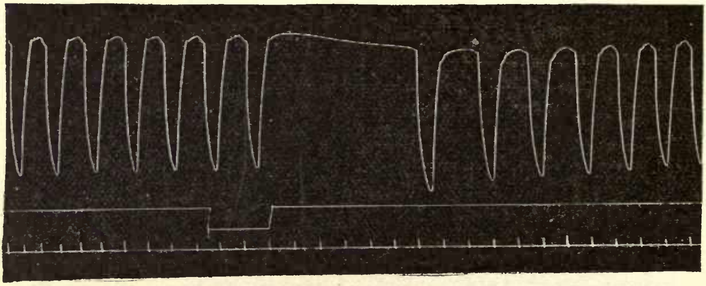


FIG. 78.—Record of the contractions of the frog's heart during stimulation of the vagus nerve. The time is given in seconds, the stimulation is indicated by the signal.

It is well to remember, however, that a heart cannot be permanently inhibited by the stimulation of the vagus nerve. Curiously enough, it again commences to beat after a few minutes of inhibition and then continues its activity in spite of the continued application of the electrical current. This phenomenon is called "escape from inhibition."

Acceleration of the Heart.—Contrary to the excitation of the vagus nerve, the stimulation of the sympathetic gives rise to an appreciable increase in the frequency and force of the cardiac contractions. It may be said, therefore, that these nerves are functionally antagonistic to one another. This fact is well substantiated by the changes following the division of the vagi nerves, because very shortly after the destruction of these paths the rate of the heart is markedly increased. It may be concluded, therefore, that this organ

is ordinarily held in check by a constant stream of minimal inhibitory impulses. Now, since the division of the vagi nerves destroys the path by means of which these restraining impulses are conducted to the heart, the frequency of this organ must be considerably increased after this procedure. This effect is considerably augmented by the pure accelerator impulses which reach the heart by way of the sympathetic nerve. The latter then gain full control over this organ. We note here a certain similarity between the action of the heart and that of a horse in harness. The horse represents a self-active mechanism which is directed along definite channels by means of reins. When the latter are slackened, the horse quickens its pace in a measure to conform more closely to its own inherent power.

B. THE REGULATION OF THE CALIBER OF THE BLOODVESSELS

The Vasomotor Mechanism.—We have previously noted that the walls of the arteries adapt themselves in a perfectly passive way to the changes in bloodpressure, giving rise to what is known as the pulse. But besides these changes which are, so to speak, forced upon them by an outside factor, the arterial wall is also able to execute movements of an active kind in actual antagonism to the internal pressure. The elements chiefly concerned in this process are the smooth muscle cells which, as has been stated above, are most numerous in the smaller arteries and are arranged here in the form of a heavy layer circularly around the lumen of the vessel. Accordingly, their contraction must diminish the size of the channel and thereby materially hinder the onward movement of the blood.

This motor mechanism is under the control of a special set of nerves which are known as vasomotor nerves. In complete agreement with the arrangement of the cardiac center, these nerve fibers originate in a colony of ganglion cells which are situated in the medulla oblongata, and comprise the so-called vasomotor center. This particular segment of the central nervous system, therefore, controls the most vital functions of our body: namely, the action of the heart,

the size of the arterial channels and, as will be brought out in a later chapter, the movements of respiration. It need not surprise us, therefore, to find that its destruction terminates life immediately, because the aforesaid vital functions are thereby made to cease. By analogy it may then be concluded that the destruction of the brain, and more especially of the cerebral cortex, need not prove fatal as long as the medulla is left intact. In the absence of the cerebral cortex the animal simply follows a non-psychic or reflex life without being deprived of its cardiac, respiratory, and vasomotor activities.

Constriction and Dilatation of the Bloodvessels.—The vasomotor center communicates by means of diverse afferent paths with practically all the sense-organs of the body. Consequently, its activity must undergo certain variations in accordance with the character of the impulses received by it. The changes to which it may give rise are of two kinds, namely, vasoconstriction and vasodilatation. The former phenomenon consists in a decrease in the size of the lumen of the bloodvessel and the latter, in an enlargement of its lumen.

The walls of the bloodvessels usually retain a position intermediate between constriction and dilatation. This statement should lead us to infer that they are ordinarily held in a state of tonus, akin to that displayed by striated muscle. It may, therefore, be surmised that the smooth muscle cells of the arterial wall are the recipients of a series of subminimal impulses which tend to keep them in a state of functional alertness and efficiency. But this state of tonus may be varied at any time in either direction by impulses of greater strength and appropriate character.

The manner in which vasoconstriction is brought about, is easily understood if it is remembered that by far the largest number of these muscle cells is arranged circularly around the lumen of the vessel. Clearly, the contraction of these elements must diminish the size of the channel and retard the escape of the arterial blood into the capillaries. Possibly the simplest way of explaining vasodilatation is to assume that the tonus impulses to the bloodvessels are inhibited. The

walls of the bloodvessels are thereby allowed to relax and to be forced outward by the internal pressure. Naturally, such an enlargement of the lumen of the arteriole must lower the peripheral resistance, and permit a larger quantity of arterial blood to enter the capillaries.

Different Vasomotor Reactions.—A phenomenon familiar to practically everybody is that of *blushing*. It is a local modification of the circulation which is usually confined to the bloodvessels of the cheeks, but may also involve a much larger area. In the light of the preceding discussion, it will now be evident that this change is dependent upon a relaxation and dilatation of these particular bloodvessels in consequence of certain psychic impressions. The impulses generated in the higher centers are relayed to the vasomotor center, whence they are distributed to the distal arteries, causing them to dilate. In consequence of the inrush of a larger amount of blood, the part so affected becomes red in color and warm to the touch.

The reverse change, namely, that of *paling*, is usually preceded by extreme terror or rage. At this time, the bloodvessels constrict and hinder the influx of blood into these channels. The part so affected loses its red color, and becomes colder to the touch.

The application of *heat and cold* produces similar reactions. Warmth relaxes the vessels, while cold constricts them. In some instances, however, this primary change is soon followed by one of opposite character. Thus, if we pass from the cold outside air into a warm room, the previously constricted bloodvessels of the exposed parts of our body relax and do not reassume their normal vascular tone until some time later. The skin then feels excessively hot.

Brief reference should also be made at this time to the fact that vasodilatation favors the escape of the body-heat, because the exposure of a large amount of blood to the colder medium, whether air or water, greatly augments heat radiation. For this reason, great care should be exercised at all times to protect the body against a fall in its temperature below its normal value of 37.1° C. (98.4° F.). A severe "chilling" of the body usually causes it to lose its vasomotor

tone and resistance against bacterial invasion. Hence, a person who has engaged in muscular exercise and whose cutaneous vessels are well filled with blood, should safeguard his body against excessive heat dissipation by putting on additional clothing.

Another very important reaction of this kind takes place in all glands whenever they are called upon to furnish an extra quantity of secretion. Activity is invariably associated with vasodilatation, because a larger amount of blood must

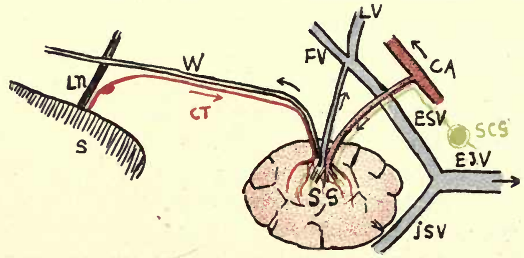


FIG. 79.—Schema illustrating the nerve supply of the submaxillary gland. *SG*, submaxillary gland; supplied by a small artery from the carotid system (*CA*). It is drained by a small vein which generally enters the facial (*FV*) at its point of confluence with the lingual vein (*LV*). The external (*ESV*) and internal (*JSV*) maxillary veins invest the gland and unite to form the external jugular vein (*EJV*). The sympathetic nerve supply is derived from the sup. cerv. ganglion (*SCG*). The chorda tympani (*CT*) attaches itself to the lingual nerve *LN* and then to Wharton's duct (*W*); *S*, lower jaw.

be brought to these parts in order to place them in the most favorable position to increase their product. While these changes are clearly in evidence in all those glands which furnish the digestive juices, a particularly interesting arrangement is present in the *salivary glands*. These organs receive a twofold nerve supply: namely, one directly from the brain and the other from the sympathetic ganglia of the thorax. Peculiarly enough, these nerves possess an antagonistic action upon the bloodsupply of these organs. If we select the submaxillary gland as an example, it will be found that its cerebral nerve or chorda tympani possesses a vasodilator action, while the sympathetic subserves vasoconstriction. Hence, it cannot surprise us to find that the excitation of the

former nerve causes the aforesaid gland to redden and to become warm to the touch, whereas the stimulation of the latter causes it to grow pale and colder. Furthermore, while the excitation of the chorda tympani gives rise to a very copious flow of a watery type of saliva, the excitation of the sympathetic yields only a very moderate amount of very thick saliva.

The bloodsupply of the abdominal organs is regulated by the greater *splanchnic nerves.* Inasmuch as these nerves contain vasoconstrictor as well as vasodilator fibers and control about one-fourth of the total amount of blood present in the body, they are in the best possible position to exert a very powerful influence upon the contents of other circulatory systems. Reference has already been made to the fact that the dilatation of the splanchnic vessels permits a certain quantity of blood to be transferred from the general circuits of the body into those of the kidneys, stomach, intestine, pancreas, spleen, and liver. Contrariwise, the constriction of these vessels causes a certain portion of their contents to be diverted into the general bloodvessels, thereby raising the systemic bloodpressure.

Another very important vasomotor mechanism is the one enabling the heart to diminish the general bloodpressure. While this organ is able to adjust the frequency and force of its beat to the arterial pressure, it may also happen at times that the resistance which it must overcome, is so great that it cannot act against it without excessive strain. Such an unusual resistance is commonly established in consequence of far-reaching vasoconstrictions, and, naturally, a heart which has been weakened by disease, is thereby placed in a position inviting injury. It possesses, however, a safety device in the shape of certain afferent fibers which are connected with the cardiac and vasomotor centers and through which a general vasodilatation and fall in bloodpressure may be occasioned. This reflex is evoked whenever the pressure within the arch of the aorta reaches a dangerous height. The resulting dilatation of the bloodvessels and fall in pressure immediately enables the heart to act with much greater freedom.

The Purpose of Vasomotor Activity.—The principal purpose of vasomotor activity is to adjust the distribution of the blood in such a way that almost any part of the body may control its own supply without necessitating a general change in the bloodflow through other organs. In other words, it permits a certain change in the distribution of the blood in favor of particular circuits quite independently of the action of the heart. Many examples, however, could be cited to show that these actions may also pursue a harmonious course. Thus, vigorous exercise not only augments the activity of the heart, but also increases the vascular tonus, thereby quickening the entire circulation.

The student should also be cautioned at this time not to confound the local effects of vasodilatation with the condition of *congestion*, because the latter usually requires for its development an obstruction to the venous return and a passive engorgement of the bloodvessels situated centrally to the block. It is to be noted, therefore, that while the congested part contains an unusually large quantity of blood, the flow through it is considerably diminished. For this reason, the blood so stagnated soon loses a large part of its oxygen, and assumes a much darker color than that exhibited by the blood in neighboring parts. The tissues containing the stagnated blood assume a dark blue appearance. It should be remembered, however, that this condition need not be localized, but may also involve much larger regions of the body, preeminently the venous system. It is a well known fact that those lesions of the cardiac valves which seriously hinder the inflow of blood into the right auricle usually give rise to a congestion of practically all the abdominal organs. This congestion is first noted in the liver and spleen, because these organs are soft in texture and quickly react to the increased venous pressure by increasing their volume.

PART III

RESPIRATION

CHAPTER XVII

THE ELEMENTARY LUNG

General Discussion.—In its widest sense the term respiration is employed to designate the interchange of the respiratory gases between the organism and the medium in which it is contained. Accordingly, the process of respiration is essentially a chemical one, because it supplies the cells with oxygen and removes from them the waste gas, carbon dioxid. It has previously been pointed out that every cell gives rise to energy which is derived from the food, but in order that the cell may be able to accomplish this end, it must reduce the nutritive substances into their simplest components by a process which requires the presence of free oxygen. Naturally, considerable amounts of this gas are taken in with the food, but the protoplasm of the cell is quite unable to utilize it when firmly united with other elements to form compounds. Hence, the oxygen must be presented to it in an available form, otherwise it cannot be used to oxidize the nutritive substances.

While it is evident that the cell burns up materials in the presence of oxygen and liberates carbon dioxid, this chemical process could not be effected without certain mechanical procedures. Respiration, therefore, also presents a mechanical aspect, embracing the transportation of the respiratory gases through the lungs and the blood. These processes are usually considered under the heading of the mechanics of respiration.

Diffusion Pressure.—The atmospheric air is a mixture of gases comprising the following constituents:

Oxygen	20.94 per cent.
Nitrogen	78.40 per cent.
Argon, krypton, neon	0.63 per cent.
Carbon dioxid	0.03 per cent.

This medium rests upon every area of the surface of our body with a certain pressure which is designated as atmospheric pressure. At this particular latitude and altitude, it is capable of supporting a column of mercury 760 mm. in height. It becomes less at a higher level and greater at a lower in accordance with the thickness of the layer of the air. This "line" of atmospheric pressure, equalling 760 mm. Hg, serves as the abscissa for all our records of pressure. Thus, when we say that the blood circulates under a pressure of 120 mm. Hg, we wish to convey the idea that this pressure exceeds that of the atmosphere by 120 mm.

It is to be noted especially that the atmospheric pressure represents the sum of the pressures exerted by its several constituents. In other words, each component of the air contributes its share toward the total pressure in accordance with its volume. Accordingly, since oxygen constitutes about one-fifth of the total volume of the air, the pressure exerted by it must amount to $\frac{1}{5}$ of 760 mm. Hg, or 152 mm. Hg. Quite similarly, since fresh air is practically free from carbon dioxid, the partial pressure of this gas in the atmosphere must be very close to zero.

Diffusion.—It is a well known fact that currents in air arise whenever areas of unequal atmospheric pressure are established. While these differences persist, the air continues to move from the place of high pressure to the place of low pressure. This movement ceases as soon as an equalization of the pressures has been attained. Quite similarly, any constituent of the atmospheric air may be made to move independently of the others by subjecting it to differences in its partial pressure. Thus, if we bring two mixtures of gases together, containing unequal amounts of oxygen, the molecules of this gas must continue to leave the one embrac-

ing it in larger quantity until its partial pressure has been equalized in the two places.

We know that an organism uses up oxygen continually and liberates carbon dioxid. Consequently, the partial pressure of the oxygen must be greater in the medium than in the organism, whereas that of the carbon dioxid must be greater within than without. In accordance with the preceding discussion, it may then be concluded that the molecules of oxygen must enter the organism, while those of carbon dioxid must leave it. The cell wall does not greatly impede the progress of these molecules, because the differences in the partial pressures of the aforesaid gases are more than sufficient to overcome this obstacle.

The Development of the Simple Lung.—It need scarcely be emphasized that the differences in the partial pressures of the respiratory gases are sufficient to establish an adequate interchange in all those organisms which consist of only a limited number of cells. Contrariwise, it may be conjectured that this process of direct diffusion must be quite inadequate if the body embraces many millions of cells and is enveloped by a relatively impermeable integument. In order to overcome this difficulty, the surface of the body has been indented in the form of a sac filled with air. This membranous pouch represents the elementary lung. In the higher animals it is suspended in the fore part of the body cavity and communicates with the outside through a narrow passage which is termed the trachea.

The distant cells of the tissues are brought in diffusion-relation with the air in this pouch through the medium of the blood. While traversing the capillary networks of the lungs the blood takes up oxygen and rids itself of a certain portion of its carbon dioxid. It then rushes to the tissues, where it transfers a part of its oxygen to the cells and acquires carbon dioxid. This interchange is repeated again and again. It will be seen, therefore, that the process of respiration consists in reality of two, namely, a diffusion between the air in the lung and the elements of the blood, and a diffusion between the latter and the cells of the different tissues. The former is called *external respiration* and the latter,

internal respiration. It is to be noted, however, that both are based upon the principle of diffusion.

The Necessity of Breathing.—It need scarcely be men-

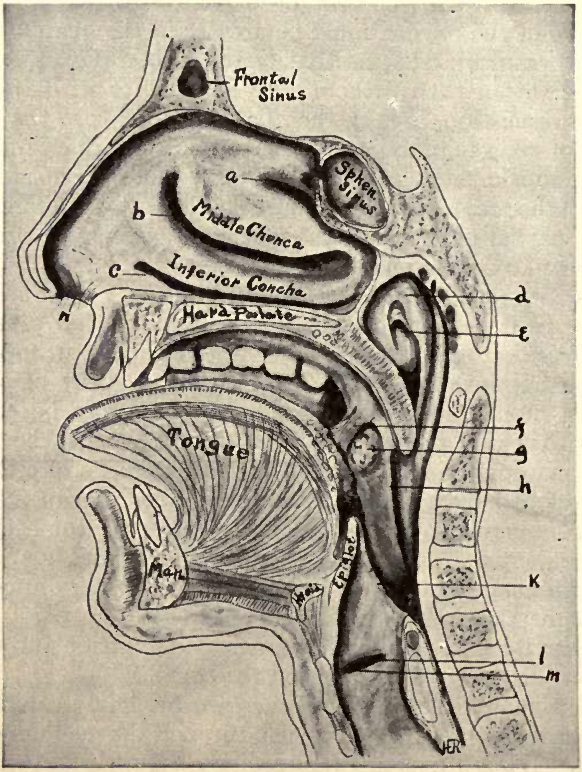


Fig. 80.—Median sagittal section through the head and neck. *a*, superior meatus of the nose; *b*, middle meatus of the nose; *c*, inferior meatus of the nose; *d*, torus tularius (eustachian cushion); *e*, orifice of auditory tube; *f*, palatoglossal fold; *g*, tonsil; *h*, galatopharyngeal fold; *k*, aryepiglottic fold; *l*, ventricle of the larynx; *m*, vocal cord; *n*, vestibule of nose. (*Radasch.*)

tioned that the continued movements of the molecules of oxygen into the blood and of the molecules of carbon dioxid into the air of the lung would eventually lead to an equaliza-

tion of the diffusion pressures and a cessation of this interchange. In other words, it would cause the death of the organism by asphyxia. Hence, in order to retain the tissues in an aerated condition, it is absolutely necessary to maintain the differences in the partial pressures of these gases, and this end can only be accomplished by the constant renewal of the air in the lung. This statement furnishes the principal reason for the act of breathing, the mechanics of which form one of the most instructive and interesting chapters in physiology.

The principle upon which the renewal of the air in the lungs is based, is a very simple one, and may be imitated very easily with the aid of a pair of bellows. When compressed, the air within this chamber is placed under a higher pressure than the atmospheric. Following the channel of least resistance, the air then escapes through the trachea to the outside. The opposite movement causes the outside air to flow into the bellows, because the pressure therein is then lower than the atmospheric. It is to be noted especially that the lung is a perfectly flaccid organ and cannot vary its capacity by active means. This statement leads us to infer that the changes in its size are to be referred to an outside factor, resident in the wall of the chest. It is to be observed that the surface of the lung is everywhere in firm contact with the thoracic wall and must, therefore, pursue the same course as the latter. The primary factor is the wall of the chest, the position of which is changed by muscular activity. Its outward movement causes the lungs to be expanded, while its inward movement causes them to be compressed. During the former phase a certain amount of air is allowed to flow into the lungs. It is again expelled during the subsequent phase of compression of these organs.

The Gills.—Very similar conditions are met with in the aquatic animals. The place of the lung is here taken by the gill-plates, representing several plate-like prolongations of tissue containing an intricate network of capillaries. They are limited externally by a layer of epithelium. As the water rushes across their surfaces a part of its free oxygen is transferred to the blood. The latter in turn gives off carbon

dioxid to the water. This oxygen is held in a free state in the water and is not derived from the watery molecule itself. Accordingly, fish are able to exist in an aquarium only in the presence of free oxygen. A very simple way of keeping the water well supplied with this gas is to allow certain plants to grow therein, because plants liberate oxygen under the influence of sunlight. It is to be noted, however, that this oxygen is of metabolic origin, *i.e.*, it is liberated in the course of the assimilative processes within the green parts of the plant, and is not expired by them.

This brings to our mind a common misconception. The idea has become prevalent that plants inhale carbon dioxid and exhale oxygen, thereby tending to maintain the composition of the atmospheric air for the benefit of animal life. While it is quite true that the existence of the animals is closely dependent upon that of the plants, it is to be noted that the consumption of carbon dioxid and liberation of oxygen by the latter is distinctly a matter of metabolism. Plants as well as animals inhale oxygen and exhale carbon dioxid, but the former require in addition carbon dioxid in order to be able to build up their substance. In the course of this process of assimilation a certain amount of superfluous oxygen is liberated which is transferred to the medium in which they are growing. This explains the very low percentage of carbon dioxid in densely wooded regions.

The Respiratory Cycle.—The phase of expansion of the lung is designated as inspiration, and its compression as expiration. Both periods together form the *respiratory cycle.* A distinct pause is not present, the chest being held either in the inspiratory or expiratory position. The number of the respiratory cycles varies in accordance with the age, sex, size and activity of the animal. Other conditions, such as the temperature of the medium, barometric pressure and season of the year also exert a distinct influence upon the rate of respiration. The adult human male respires about 16 times in a minute, and the human female 17 to 18 times. Muscular exercise increases the respiratory frequency considerably, because a larger amount of oxygen is then needed to satisfy the metabolic requirements of the body, while a

larger amount of carbon dioxid is liberated. Small animals respire more frequently than larger ones, because they suffer a greater loss of heat in comparison with the mass of their body. A loss of heat can only be compensated for by a correspondingly greater production of heat, *i.e.*, by activity and more intense oxidations. Increases in the body-temperature are usually associated with a greater respiratory activity. Lowering the outside temperature produces a similar result, because the greater loss of heat occasioned thereby must be balanced by intensifying the metabolism of the tissues. For this reason, the mammals, with the exception of the hibernating animals, are more active during the winter months and consume at this time much larger amounts of food.

CHAPTER XVIII

THE MECHANICS OF RESPIRATION

The Larynx and Trachea.—The respiratory mechanism of the mammals consists of the lungs, one on each side of the body, and a passage by means of which communication is established with the outside air. Entrance to this passage is gained either through the nose or mouth. These chambers open posteriorly into a common space, the *pharynx*, whence the windpipe or *trachea* leads downward through the

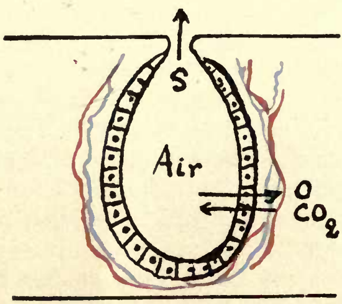


FIG. 81.—Diagram of an elementary lung. *S*, stigma; *O*, oxygen diffusing from air of saccule into tissue fluids; CO_2, diffusing in reverse direction.

anterior region of the neck. Opposite the second pair of ribs it divides into two tubes, known respectively as the right and left bronchus. The pharyngeal cavity is continued onward as the gullet or *esophagus*, a membranous tube which lies directly behind the trachea and traverses the entire length of the chest to gain access to the stomach.

The uppermost segment of the trachea is modified to form a special organ for phonation, which is known as the *larynx*. Entrance to this cavity is gained through an aperture which

is guarded by a leaf-like lid, called the *epiglottis*. The food entering the pharynx is projected downward into the esophagus and cannot escape into the respiratory passage, because the orifice leading into the larynx is at this time at least partially closed. It should be noted, however, that the epiglottis is not the only factor concerned in this closure, because the entrance of food into the trachea is already guarded against by the backward movement of the tongue and the elevation of the larynx. Nevertheless, it cannot be denied that the epiglottis serves as a special means of shutting out fluids and liquefied foods.

It is also to be observed that the respiratory movements are inhibited during the act of swallowing, so that the food cannot be drawn into the larynx. When, however, the acts of swallowing and inspiration are not properly correlated, small particles of food and liquids may be diverted into the respiratory channel and give rise to an intense irritation of its lining membrane. This excitation induces the act of coughing, a reflex contraction of the expiratory muscles furnishing a powerful blast of air which is forced through the cavity of the mouth. Its purpose is the dislodgment of the irritating particle. The same principle is involved in the act of sneezing. In this case, however, the air is diverted through the nasal cavity.

A short distance below the epiglottis lie the *vocal cords*, two transverse bands of fibrous tissue which project far into the lumen of the laryngeal cavity. Their position and structure permits them to vibrate in consequence of the impacts produced by the expiratory blasts of air. The sounds produced by these membranous bands are modified by the vibration of other parts, such as the walls of the chest and larynx, the epiglottis, pharynx, and membranous structures situated above this cavity. It will be seen, therefore, that the phonating organ of the mammals is constructed after the principle of an ordinary blow-instrument, such as a trumpet. The essential part of the latter is a tube, the orifice of which is partially closed by a transverse strip of thin metal. By blowing forcibly through this tube the aforesaid band is made to vibrate and to produce oscillations of a similar

character in the neighboring air. The latter are conveyed into consciousness through the agency of the ear.

Sounds of high and low pitch are occasioned by varying the tenseness of the vocal cords, because when thoroughly tightened these bands cannot vibrate so freely as when relaxed. Changes of this character follow one another in rapid succession during the production of coördinate sounds, such as are used in speaking. They are caused by finely adjusted movements of the cartilages of the larynx in consequence of the contractions of special sets of muscles.

The trachea is a firm, resistant tube, consisting of a series of rings of cartilage which are joined at their edges by membranous septa. This tube measures about four inches and a half in length and about three-quarters of an inch in diameter. The first ring is modified to aid in the process of phonation and forms, therefore, a part of the larynx. It is known as the *cricoid cartilage.* Posteriorly, where the trachea lies in contact with the esophagus, the cartilaginous rings are incomplete and flattened. In spite of this structural deficiency, however, the tube as a whole possesses a resistance sufficient to prevent its collapse under the varying degrees of pressure established by the respiratory movements.

The Bronchi and Lungs.—Opposite the fourth dor al vertebra the trachea divides into two smaller tubes which are termed the *bronchi*. Immediately upon their entrance into the lung, these tubes break up into a number of smaller ones, which are designated as *bronchioles*. The smallest of these are without cartilaginous support and terminate in elongated saccules, called *infundibula*. Each infundibulum is divided by incomplete partitions into a number of smaller compartments which are termed *air-cells* or *alveoli*.

Thus, it will be seen that the mammalian lung possesses certain structural peculiarities which cause it to resemble very closely the lung of the lowest forms. Inasmuch as the infundibulum corresponds really to the greatly dilated end of the bronchiole, it may justly be compared to the pouch-like lung of the amphibians. It should be remembered, however, that the long diameter of these air-spaces measures less than 1.0 mm. ($\frac{1}{30}$ of an inch), whereas the length of the

expanded lung of a frog of medium size amounts to about 4 cm. (1½ inches). The alveoli are still smaller in size, measuring on an average only about 120μ in length, but since there are about 400 millions of them in each lung, the total surface presented by them to the respiratory air is surprisingly large. Approximate measurements have shown that the capillaries of the lungs possess an aggregate surface of about 125 sq. m. (300 square feet). Since the surface

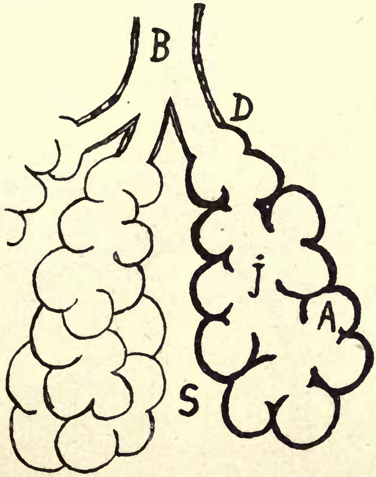


Fig. 82.—Diagram illustrating the arrangement of the infundibula. *B*, bronchiole; *D*, infundibular duct; *J*, infundibulum; *A*, alveolus; *S*, interinfundibular space, occupied by capillaries.

of the body of a man of medium size measures only about 1.25 sq. m. it will be seen that the sheet of blood exposed to the air in the lungs for purposes of diffusion, is almost 100 times as large as that of the body-surface. These figures are only approximately correct and are given here merely to impress upon the reader the enormous size of the layer of blood engaged in external respiration.

The different infundibula are bound together to form *lobules*, and several lobules to form a *lobe*. The right lung consists of three lobes, and the left one of two. The external

surface of each is invested by a serous membrane, known as the *pleura*. This lining is reflected from the root of each organ to cover the entire internal surface of the wall of the chest. Thus, the pleura really consists of two layers: namely, one upon the surface of the lung and one upon the inner aspect of the thoracic wall. The former is designated

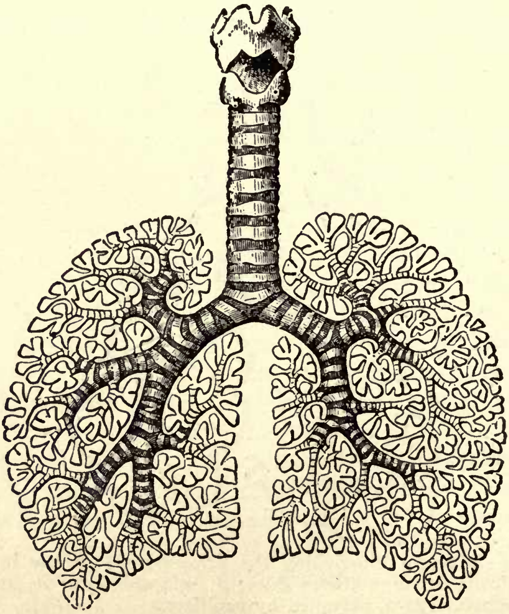


FIG. 83.—Human respiratory apparatus showing the branching of the bronchi in the interior of the lungs. (*Duval.*)

as *visceral pleura*, and the latter, as *parietal pleura*. Their opposing surfaces lie in firm contact with one another, and are moistened with a small quantity of a serous secretion which is termed the *pleural fluid*. The purpose of the latter is to prevent friction while the lungs change their size and position during the successive respiratory phases.

The Thorax.—The cavity of the thorax is a subdivision of the cavity of the trunk, its floor being formed by a musculo-tendinous septum which is called the *diaphragm*. This

membrane is stretched transversely across this cavity about opposite the lower tip of the sternum. The thorax exhibits a conical outline, its tapering upper expanse advancing as far as the base of the neck. Posteriorly, it is limited by the spinal column, laterally by the ribs, and in front by the sternum. The lungs occupy this entire space with the exception of its median extent which gives lodgment to the heart and large bloodvessels, and is designated as the mediastinum.

It will be seen, therefore, that the lungs are situated in a closed compartment, and communicate with the outside only through a relatively narrow passage, the trachea. Their surfaces lie everywhere in intimate contact with the inner surface of the thoracic wall. This position they must retain, because the pleural space is closed and thoroughly protected against the atmospheric air by the ribs and adjoining intercostal muscles and membranes.

A separation between the outer surface of the lung and the chest wall can only be effected by the establishment of a free communication between the pleural cavity and the outside. The air entering through this opening into the formerly potential pleural space, permits the lung tissue to draw away from the wall of the chest. This property of recoil is resident in the elastic fibers of the walls of the alveoli. Inasmuch as every air-sac is thereby greatly reduced in size, the volume and capacity of the entire organ must also be considerably diminished. This phenomenon is designated as the *collapse of the lung*. When in this state, the lung can no longer be expanded in the normal way, because it now lacks the force of the chest wall acting upon its external surface. But, a collapsed organ is not entirely free from air, because the walls of the membranous bronchioles are brought together before the air has had sufficient time to escape from the alveoli. Consequently, a collapsed lung will float, and is able to carry a considerable weight in addition to its own. The collapse of one lung does not necessarily prove fatal, because this loss is compensated for by a more complete expansion of the opposite organ.

The Expansion of the Lung.—In order to be able to understand the manner in which the lungs are expanded, the

following points already alluded to above, should be kept firmly in mind:

(*a*) The surface of the lung is kept in absolute contact with the internal surface of the wall of the chest.

(*b*) The lung is a perfectly passive organ and possesses no means by which it could increase or decrease its size and capacity in an active way.

(*c*) The active factor in respiration is the wall of the chest. It is moved outward during inspiration by the contraction of certain muscles, forming the group of the

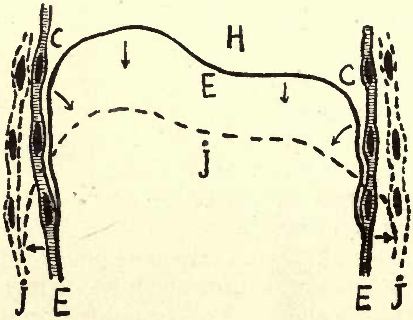


Fig. 84.—Diagram showing the position of the diaphragm and adjoining wall of the trunk on inspiration and expiration. *E*, expiration; *J*, inspiration. The diaphragm moves downward and the walls of the trunk outward, increasing the size of the complementary space *C*. The slight depression at *H* is caused by the apical portion of the heart.

inspiratory muscles. When these muscles cease to contract, the wall of the chest returns into its original position. This movement constitutes the expiratory phase of the respiratory cycle. We shall see later that inspiration is an active process throughout, whereas expiration is passive under ordinary circumstances, *i.e.*, it is accomplished by gravity and elastic recoil and not by the contraction of a special set of muscles.

Having established this principle, that these movements of the wall of the chest are responsible for the variations in the size of the lungs, let us briefly analyze the manner in which the capacity of the thorax is altered. In the first place, do not expect to find very striking fluctuations, because nature

always works efficiently with the least expenditure of energy. Thus, while it is apparent in most animals that the size of the chest is larger during inspiration than during expiration, this difference is not considerable under ordinary circumstances. It should also be noted that the chest is enlarged in all directions, but chiefly in three: namely, from above downward, from before backward, and from side to side.

The increase in its height is produced by the contraction of the *diaphragm*. This membrane consists of a central tendinous portion, to the margin of which are attached the different muscle fibers. The latter pursue a course radially downward and are finally attached to the inner surfaces of the lower ribs. Accordingly, this musculo-tendinous septum presents a curved outline, its convexity being turned into the cavity of the chest. It will be seen, therefore, that the contraction of its muscle fibers must pull its tendinous portion downward, thereby increasing the vertical diameter of the chest at the expense of that of the abdominal cavity.

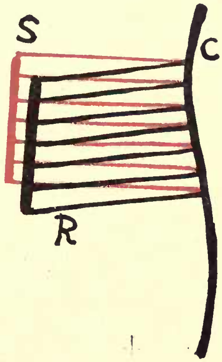


FIG. 85.— The position of the ribs on inspiration (red) and expiration (black). *S*, sternum; *C*, spinal column; *R*, ribs.

The antero-posterior and transverse diameters of the chest are increased by the upward movement of the sternum and ribs. The latter are hinged upon the vertebræ and are united with the sternum by means of short pieces of cartilage. However, since the hinder end of each rib articulates with the corresponding vertebra in two places, its movements cannot take place in a straight line up and down, but must follow the oblique axis of rotation of these joints. For this reason, the upward movement of each rib necessitates a moderate outward rotation of its bony portion at the angle and a slight torsion of its cartilaginous sternal end.

At the end of expiration the ribs are directed obliquely downward, so that the sternum assumes a much lower level than after the completion of inspiration. Ordinarily, the

range of this movement is sufficient to permit the rib below to assume the level of the next rib above. Now, since the horizontal diameters of the chest increase from above downward, this elevation of the sternum must bring the larger areal expanse of the chest at the rib below to that of the next rib above. Moreover, since the ribs are relatively inflexible, their upward movement must push the sternum forward, thereby increasing the diameter of the chest from before backward.

The Deflation of the Lung.—The three factors which should be held responsible for the decrease in the size of the lung, are gravity, elastic recoil, and muscular action. As has been stated above, normal expiration is very largely a passive act and is not participated in by any muscles with the possible exception of the internal intercostals. However, when the gas interchange is to be hastened, other muscles are called into play until even the expiratory movement becomes distinctly active. Thus, it may be stated that the hard parts are carried into their former position by their own weight as soon as the inspiratory muscles have ceased to act upon them. Besides, the cessation of the inspiratory effort permits the parts previously put on the stretch to recoil until they have assumed their former positions. Lastly, certain muscles may be activated during the expiratory phase in an endeavor to hasten the inward movement of the chest wall.

This action is well illustrated by the movements of the diaphragm. When this muscular septum contracts during inspiration, it is flattened and encroaches upon the space of the abdomen. The abdominal organs are thereby put under a certain pressure, while the lung tissue is pulled upon and expanded. Now, since, the abdominal cavity is limited posteriorly by the unyielding vertebral column and below by the pelvis, an interchange of pressure can only be accomplished through its soft anterior and lateral walls. Accordingly, we find that the downward progression of the diaphragm and neighboring liver and stomach causes the abdominal wall to be pushed outward. The connective tissue and muscles of the latter are thereby put on the stretch. Immediately upon the completion of the contraction of the

diaphragm, these parts recoil and force the abdominal viscera back into the space vacated by the lung. Hence, the upward movement of the diaphragm, is accomplished by two factors: namely, the pull exerted upon its upper surface by the recoiling lung and the push imparted upon its under surface by the recoiling abdominal wall.

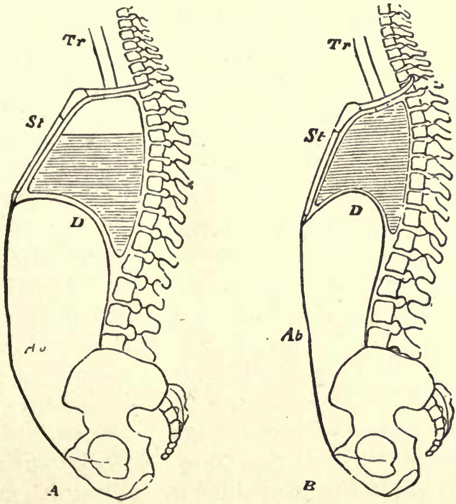


FIG. 86.—Diagrammatic sections of the body in *A*, inspiration; and *B*, expiration; *tr*, trachea; *st*, sternum; *D*, diaphragm; *ab*, abdominal walls. The shading roughly indicates the stationary air. (*From Huxleys "Lessons in Elementary Physiology," Macmillan Co., Publishers.*)

Diaphragmatic and Costal Breathing.—Under ordinary circumstances the descent of the diaphragm is sufficient to yield an adequate interchange of the gases, but when a more ample ventilation of the lungs is to be effected, the action of this muscle must be augmented by that of other respiratory muscles. The normally *diaphragmatic* type of respiration is then changed into one possessing a distinct costal character. Naturally, this change necessitates the participation of the upper ribs in respiration. Costal respiration is usually said to be characteristic of woman, and diaphragmatic respiration of men, but this distinction is not based upon physiological

differences, because those women who are not in the habit of wearing corsets, likewise respire chiefly with the aid of the diaphragm. In accordance with the preceding discussion, it may be concluded that costal respiration must be resorted to whenever the descent of the diaphragm is hindered. Such an impairment may easily be brought about by sitting in a cramped position in a chair, and especially when the stomach is well filled with food.

The successive involvement of the different muscles of respiration may easily be observed in a person indulging in physical exercise. To begin with, solely the diaphragm and lower intercostal muscles are at work, while later on the gradually increasing metabolism necessitates the simultaneous activation of the upper intercostals and accessory muscles of respiration. No doubt, everyone of us is familiar with the picture presented by a person who has just completed a long-distance race. We are impressed by the set character of his face, his opened angular mouth, the cord-like prominence of the sterno-cleido-mastoid muscles, and the forward bend of his neck and shoulders. All these muscular actions favor the fixation of the upper ribs, so that it becomes possible to act upon the others with much greater force. Similar fixed points are established at this time below, but principally by the quadrati lumborum and allied muscles which give support to the lower ribs.

Normal and Forced Breathing.—In accordance with the preceding discussion, it may be concluded that the respiratory movements may present either a *normal* or a *forced* character. As long as the metabolism retains a moderate intensity, the diaphragm with the possible addition of the lower intercostals, suffices to give an adequate ventilation of the lungs and interchange of the gases. Contrariwise, a constantly increasing number of respiratory muscles must be brought into play when the metabolism is augmented. The forced inspiratory movements are then associated with forced expirations, necessitating the participation of the different muscles of expiration.

The action of the diaphragm is augmented first of all by the *intercostal muscles*, consisting of two layers of fibers which pass

between the successive ribs in opposite directions to one another. Those of the external layer pursue a course obliquely downward and forward to the rib below, while those of the internal layer run obliquely upward and forward to the rib above. Their contraction keeps the intercostal spaces in a firm condition, so that these relatively soft areas of the chest wall cannot be drawn inward by the recoil-

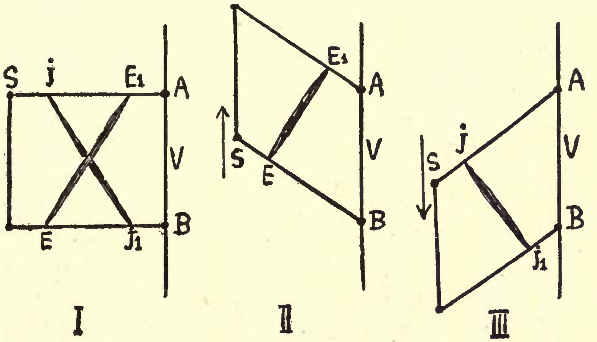


FIG. 87.—Diagram illustrating the action of the intercostal muscles. S, sternum; V, vertebrae; A and B, two consecutive ribs; EE_1. external intercostal muscle; II_1, internal intercostal muscle. The contraction of the first raises the ribs (II), while the contraction of the second lowers them (III). The distance SV is now shortened.

ing lung tissue. Secondly, they exert a very characteristic action upon the position of the ribs, because the external fibers move them upward while the internal ones depress them. In explaining these movements it should be remembered that the contraction of a muscle brings its point of insertion closer to its point of attachment. Now, since the points of attachment of the external fibers lie nearer the vertebral column than their points of insertion upon the rib below, their contraction must move the sternum upward. Likewise, since the points of insertion of the internal fibers upon the rib above are situated farther away from the spinal column than their points of attachment, their contraction must pull the sternum downward. The raising of the ribs is aided in all probability by other muscles, but principally by the levatores costarum.

CHAPTER XIX

THE CHEMISTRY OF RESPIRATION

The Effect of the Respiratory Movements upon the Air Content of the Lungs.—It need scarcely be emphasized that the inspiratory expansion of the lungs produces an area of low pressure within the pulmonary passages, whereas the expiratory movement places the air in these channels under a higher pressure than the atmospheric. In consequence of these changes in pressure a certain amount of air is made to flow into the lungs with each inspiratory phase. This air is again expelled during the succeeding expiratory period. It will be noted, however, that the quantity of air actually moved during each respiratory cycle is small in comparison with the total amount of air present in the lungs.

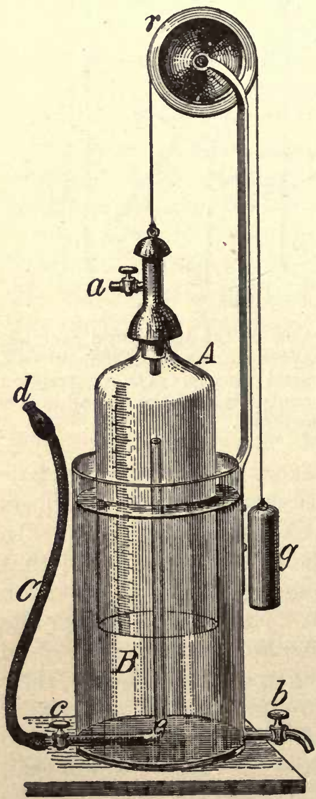


Fig. 88.—Wintrich's modification of Hutchinson's spirometer. (*Reichert.*)

This point may easily be proved by measuring the volume of the respiratory air by means of an instrument which is modelled after an ordinary gasometer and is known as a *spirometer* (Fig. 88). This instrument consists of a cylinder (*B*) filled with water, in which

is suspended a smaller cylinder (*A*) containing air. The weight of the latter is accurately counterpoised (*G*), so that it moves with the least possible resistance. The tube (*C*) enters through the outside cylinder and is continued upward to the level of the water in the inside compartment. When air is expired through this tube, cylinder *A* rises, its excursion being registered by a pointer resting upon a scale.

By means of the spirometer it has been ascertained that a normal adult inspires each time only about 500 c.c. of air, which is designated as the *tidal air*. Under ordinary circumstances this amount is added to about 3000 c.c. of air which is always retained in the lungs. The latter is called *the stationary air*. If, however, a forced expiration is resorted to, the person is able to exhale 1500 c.c. in addition to the tidal air. This extra quantity is termed the *supplemental air*. Thus, the stationary air is really made up of 1500 c.c. of supplemental air and 1500 c.c. of *residual air*, the latter constituting that portion of it which cannot be expelled even by most powerful expiration. It is also possible to inspire very deeply, and to take in 1500 c.c. in addition to the tidal air. This extra amount is called the *complemental air*.

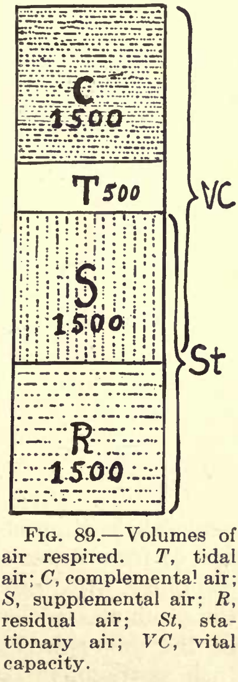


FIG. 89.—Volumes of air respired. *T*, tidal air; *C*, complemental air; *S*, supplemental air; *R*, residual air; *St*, stationary air; *VC*, vital capacity.

Consequently, an adult person of medium size is able to accommodate about 5000 c.c. of air in his lungs. This amount constitutes the *total lung capacity*. The sum of the supplemental, tidal and complemental air amounts to 3500 c.c. It reveals the *vital capacity of the lungs*, a factor frequently made use of in ascertaining the functional power of the thorax.

The Changes in the Respired Air.—When a comparison is made between samples of expired and inspired air, it will

be noted that they differ from one another in a chemical as well as physical way. Ordinary atmospheric air contains in 100 volumes: 20.96 per cent. of oxygen, 79.00 per cent. of nitrogen, and 0.04 per cent. of carbon dioxid. Expired air, on the other hand, embraces only 16.50 per cent. of oxygen, 79.50 per cent. of nitrogen, and 4.0 per cent. of carbon dioxid. Accordingly, it will be seen that the inspired air loses about 4.0 per cent. of oxygen, and gains a corresponding amount of carbon dioxid. The slight gain in nitrogen is due to the fact that the expired air is always contaminated with mucous and cellular particles which have been torn loose from the respiratory passage.

Among the physical differences should be mentioned the fact that the expired air is always warmer than the inspired, but whether the former is actually heated to the temperature of the body depends upon the initial temperature of the air taken in as well as upon the length of time during which it is retained in the lungs. Secondly, the expired air invariably contains a larger amount of water vapor, which is derived chiefly from the lining of the outer respiratory passage. The quantity of water which may be lost by the body in this way, often amounts to 300 c.c. in the course of twenty-four hours. Thirdly, the volume of the expired air is somewhat smaller than that of the inspired ($\frac{1}{50}$), because a moderate portion of the oxygen taken in unites with hydrogen to form water. Accordingly, not all the oxygen inhaled combines with carbon to form carbon dioxid, otherwise the amounts of these gases would be accurately balanced. Lastly, the expired air embraces certain organic admixtures, such as fragments of the lining of the respiratory passage, and mucus. While these constituents form a distinctly injurious element in expired air, they should not be held responsible for the repulsive odor sometimes emitted by the breath. Such odors usually find their origin in decaying particles of food and in the putrefying emissions of chronically inflamed areas of the nasal and pharyngeal cavities.

Attention should also be called at this time to the fact that while only a comparatively small quantity of air is moved with each respiratory movement, the total amount respired

in the course of twenty-four hours equals about 10,000 liters, or 350 to 400 cubic feet. From this astonishingly large volume of air the body abstracts its oxygen. When calculated at 4 per cent., the latter equals about 500 liters, or 18 cubic feet. It need scarcely be emphasized that these figures are greatly increased during muscular exercise.

The Interchange of the Respiratory Gases.—It has been noted above that the lungs are only partially deflated during expiration and retain about 3000 c.c. of stationary air after each ordinary expiration. How then is the tidal air able to reach the blood, when this amount of air is barely large enough to fill the outer respiratory passage? This question may be answered satisfactorily by simply applying the principles of the laws of diffusion to the mammalian lung.

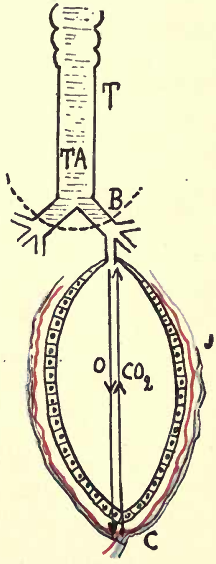


FIG. 90.—Diagram illustrating the diffusion of the gases between the tidal air and the blood. *T*, trachea; *TA*, tidal air; *B*, bronchi; *J*, infundibulum; *C*, capillaries; *O*, oxygen atoms; CO_2, molecules of carbon dioxid.

The tidal air in the outer respiratory channels possesses practically the same composition as the atmospheric air. Consequently, its molecules of oxygen must be held under a partial pressure of 152 mm. Hg, while those of carbon dioxid must be under a partial pressure only slightly above zero. In the blood, on the other hand, the partial pressure of the oxygen must be much lower, namely, something like 100 mm. Hg, whereas that of carbon dioxid must be high, approaching the value of 35 mm. Hg. Hence, the molecules of oxygen must flow in a steady stream from the tidal air into the blood, where they combine with the hemoglobin of the red cells to form oxyhemoglobin. Contrariwise, the molecules of carbon dioxid must leave the blood and pass into the tidal air. These diffusion streams continue as long as the differences in the partial pressures

of these gases are kept up by the successive inspiratory renewals of the air in the outer respiratory passage. Nitrogen is an inert gas, and merely serves as the medium in which this diffusion is accomplished.

Eupnœa, Apnœa, Dyspnœa and Asphyxia.—Whenever normal amounts of oxygen are taken in and normal amounts of carbon dioxid given off, the body is said to be in equilibrium as far as these gases are concerned. The respiratory movements then possess a normal frequency and amplitude. At this time the body is in the condition of *eupnœa.*

The condition of *apnœa* signifies a superfluity of oxygen. Whenever the system contains too large an amount of this gas, the respiratory movements are discontinued until it has again been reduced to its normal value. Apnœa, therefore, is characterized by a cessation of the respiratory movements. It is a matter of common experience that this condition may be produced very easily by respiring three or four times in quick succession: The breath is then held until the excess oxygen has been used up. Apnœa may also be induced by inhaling air containing a larger amount of oxygen than usual. The partial pressure of this gas is thereby increased, causing its molecules to enter the system at a much faster rate than normal.

The condition of *dyspnœa* signifies a scarcity of oxygen, and superfluity of carbon dioxid. It is characterized by an increased respiratory rate and force. Dyspnœa may be produced by mechanical as well as chemical means. Thus, it is easily conceivable that a poorly ventilated state of the alveolar contents and diminished intensity of diffusion must follow the partial occlusion of the trachea by foreign bodies and tumors. The same result may be obtained by the inhalation of an inert gas. Carbon monoxid belongs in this group of agents, because it prevents the ingo of oxygen by uniting with the hemoglobin of the red cells to form carbon-monoxid-hemoglobin. A corpuscle so altered loses its properties as a carrier of oxygen, because the aforesaid combination of hemoglobin and carbon monoxid cannot easily be destroyed.

During the later stage of dyspnœa convulsive muscular movements set in which are associated with intense inspira-

tory efforts. After the oxygen supply has been completely exhausted, these spastic inspirations recur at long intervals and finally cease altogether. The heart stops beating very soon afterward, its right side as well as the central veins then being greatly distended with very dark blood. This advanced stage of dyspnoea is designated as *asphyxia.* It indicates a deprivation of oxygen and an excessive accumulation of carbon dioxid.

The foregoing discussion should allow us to form an opinion regarding the manner in which such diseases as pneumonia terminate life. Pneumonia is an inflammatory reaction of the substance of the lung, as against pleurisy which is an inflammation of its outer lining membrane. In the course of this disease the lining cells of the alveoli give off a certain amount of exudate which accumulates in the infundibular spaces until the latter have been completely blocked. Obviously, this infiltration must render these spaces functionally useless, because the ordinary partial pressure of the oxygen then no longer suffices to drive this gas through the exudated material. Dyspnœa sets in as soon as a sufficient number of alveoli have thus been rendered functionally useless. Under favorable circumstances, this stage during which parts of the lungs are solidified, is followed by the stage of resolution. The exudated material is again absorbed, thereby permitting the molecules of the gases to traverse the alveoli in normal numbers.

Ventilation.—The object of ventilation is to make indoor conditions suitable for indoor life. Consequently, the problem involved in ventilation is essentially a physiological one and must have as its primary object the chemical composition of the air breathed. The temperature and content in water vapors of the latter are really of secondary importance, although as high a percentage as 0.3 to 1.0 of carbon dioxid may readily be endured, if the air is cool and relatively dry. We have previously noted that an adult person inhales about 500 c.c. of air seventeen times in a minute, and that his output of carbon dioxid at rest amounts to 17 liters or 0.68 cubic foot in an hour. If the normal amount of this gas is 0.03 per cent., its percentage in 28,000 liters or 1000 cubic

feet will be increased to about 0.1 per cent. in the course of one hour. Consequently, the amount of fresh air required per hour to keep the carbon dioxid at 0.06 per cent., is $0.03:0.68:100:x$, or $x = 2000$ cubic feet. In this calculation an allowance should be made for the size of the person and the kind of work performed by him.

It is also of interest to note that rather high percentages of carbon dioxid may be endured without great discomfort, provided the air is cool and relatively dry. Optimum conditions prevail when its carbon dioxid content does not exceed 0.06 per cent. and when its temperature is between 65 and 68° F. with a relative humidity of 50 to 75 per cent. Cold stimulates the cutaneous sense-organs, and augments the tonus of the bloodvessels as well as that of the heart muscle. The circulation is intensified. A warm and stuffy atmosphere, on the other hand, relaxes and gives rise to symptoms of fatigue and exhaustion in spite of the fact that its content in carbon dioxid may be low.

It need scarcely be emphasized that air containing a large amount of water vapor, prevents the moisture upon the surface of the skin from evaporating, and hinders thereby the body in discharging its heat in this manner. Likewise, a high temperature of the surrounding air diminishes the loss of heat from the lining of the pulmonary passage. Both factors combined greatly favor heat-retention and eventually produce those uncomfortable sensations which practically everybody experiences under these circumstances. The production of currents in the air by electric fans and other means diminishes this discomfort, because it increases heat-dissipation by constantly bringing fresh air in contact with the surface of the body.

The Respiratory Interchange at High Altitudes.—As we ascend to a higher altitude, the barometric pressure gradually decreases, reaching a value of about one-half the coast standard at a height of 15,000 feet. In accordance with the laws of diffusion, this decline in the atmospheric pressure and partial pressures of the constituents of the air must impair the influx of the oxygen, because the molecules of this gas are now under a driving power considerably less than

152 mm. Hg. Clearly, the fact that the hemoglobin of the red cells possesses a natural affinity for this gas, cannot alter this result, because the readiness with which these elements combine is not augmented at higher levels in a measure to counteract the effect of the loss in partial pressure.

This difficulty is overcome in a large measure by the formation of many new red corpuscles. Thus, it appears that the scarcity of oxygen arising at high altitudes stimulates the corpuscle-producing organs to greater activity, thereby placing the blood in possession of a greater number of oxygen carriers. When this physiological reaction is at its height, the red-cell-count may be something like 8,000,000 per cubic millimeter of blood, as against the normal of 5,000,000 per cubic millimeter. Obviously, this change must influence the interchange of the oxygen in a very beneficial manner, because while each corpuscle now contains a somewhat smaller amount of this gas than at a lower altitude, the total amount of the latter cannot be materially diminished in view of the fact that the number of the carriers has been considerably augmented. At still higher levels, however, an adequate interchange of oxygen cannot be effected even with the aid of this physiological reaction, because the partial pressure of this gas is then so greatly reduced that the aforesaid compensation becomes entirely ineffective. The complex of symptoms frequently experienced at high altitudes, constitutes the so-called *mountain sickness*. Heights of 5000 to 6000 m. cannot well be endured by most people. Still greater heights can only be reached with the aid of pure oxygen.

It should be borne in mind, however, that the breathing of pure oxygen by a healthy person is not without its dangers, because excessive amounts of this gas possess a poisonous action upon the cells of the tissues. This statement implies that the activity of normal living matter cannot be augmented by "forced draft," as a fire might be. Oxygen serves as a potent remedial agent only when the quality of the blood is to be restored within a comparatively brief period of time. For this reason, pure oxygen is frequently administered in pneumonia and other respiratory diseases when, owing to the poor ventilation of the alveoli, its percentage in the blood

has been greatly diminished. A similar reason may be given for the administration of oxygen during ether narcosis. It mitigates the after-effects of this narcotic agent in an unmistakable manner. When carefully administered, oxygen also increases the power of resistance of long-distance runners and swimmers.

The Respiratory Interchange at Low Altitudes.—Pressures higher than the atmospheric must be endured by all those persons who are engaged in the construction of tunnels and piers for bridges or in deep-sea diving. It may then become necessary to fill the compartments in which these men are working with compressed air so as to balance the pressure of the water. At a depth of 34 feet the air pressure must be twice as great as the atmospheric, and at 68 feet three times as great; in fact, pressures varying between four and five atmospheres are often required in work of this kind. In order to become accustomed to these high pressures, the person usually passes through several chambers, in which the air is held under increasingly greater pressures. The same procedure should be followed in leaving the place of high pressure, because if the decompression is accomplished too hastily, the person is prone to develop the so-called *caisson disease*, or, as the workmen call it, the "bends." As the name suggests, one of its principal symptoms is severe muscular pain which is associated with muscular spasms; in fact, it may also be characterized by a paralysis of certain groups of muscles. The name usually applied to the latter symptom is diver's palsy.

The principal danger associated with work under high degrees of barometric pressure, does not seem to lie in a disturbance of the interchange of the oxygen or carbon dioxid, but in that of the nitrogen. Obviously, the amount of this gas present in the system must be considerably increased at lower levels, for as this gas does not possess a distinct respiratory function, its molecules must be held in the body-fluids in physical solution. Further, the number of the molecules of nitrogen in these fluids must be much greater at low levels than at high levels. If the person now passes from a place of high barometric pressure (low level) into one in which the

pressure is less (higher level), these molecules of nitrogen must seek to escape in the direction of least resistance. No disturbances of function result when the decompression is accomplished in a very gradual manner, whereas a quick decompression invariably causes these molecules to break directly through the tissues. In this way, certain ganglion cells and nerve fibers are frequently destroyed which subserve muscular motion. A paralysis of the muscles innervated by these cells must be the result of such an injury.

CHAPTER XX

THE NERVOUS REGULATION OF RESPIRATION

The Respiratory Center.—The activity of the different muscles of respiration is controlled by a special group of nerve cells, situated in the medulla oblongata. This center communicates with the aforesaid muscles by means of a number of efferent nerves, and is itself connected with different sense-organs by numerous afferent paths. The principal efferent channels are formed by the phrenic nerves which control the action of the diaphragm, the most important muscle of inspiration. It will be seen, therefore, that the general arrangement of the mechanism controlling the respiratory movements is practically the same as that regulating the action of the heart and the caliber of the arteries. The cells of this center discharge impulses at regular intervals which cause certain groups of muscles to contract, thereby instigating the inspiratory movement This phase of muscular activity is immediately followed by the largely passive expiratory movement.

In further analysis of this subject-matter, our attention should next be directed to the cause of the orderly sequence of the respiratory movements and the variations in the frequency and depth of these movements resulting in consequence of afferent stimuli. The lungs are essentially a pair of bellows which may be expanded either at a fast or a slow rate, and either at regular or irregular intervals. Their expansion, as has just been stated, is occasioned by impulses discharged by the center. Whenever these impulses are blocked, respiration must cease. Accordingly, it may justly be assumed that the action of the respiratory center is automatic, *i.e.*, it takes place in consequence of certain inherent stimuli. This primary automatism, however, is subject to all sorts of influences and in a much greater degree than that

of the cardiac mechanism. This conclusion is justified upon the ground that the activity of the heart continues even after its connections with the central nervous system have been destroyed.

The Regulation of the Respiratory Movements.—The foregoing discussion must have shown that the variations in the frequency and depth of the successive respiratory movements originate in changes in the number and character of the efferent impulses discharged by the center. The only question that remains to be answered as yet, pertains to the nature of the cause producing these differences in the functional capacity of the center. Experimentation has proved that the chief factor is the quality of the blood, and, naturally, the only characteristic that need be considered in this connection is its oxygen and carbon dioxid content. It is easily conceivable that an augmentation of the respiratory movements must result whenever the percentage of the former gas is diminished or that of the latter increased. Animal experimentation again has shown that the carbon dioxid is the more important factor of the two, because the slightest possible increase in the percentage of this gas in the blood gives rise to a very decided increase in the rate and depth of the respiratory movements. Thus, carbon dioxid really plays the part of a specific stimulant of the respiratory center. When its percentage in the blood is raised, the constituents of the repiratory center immediately react toward this change by evoking more frequent and powerful contractions of the respiratory muscles.

The second question pertains to the nature of the mechanism by means of which the individual respiratory movements are made to retain a definite length and to follow one another at perfectly regular intervals. During its descent through the neck and thorax the vagus nerve gives off several branches. Two of these, namely, the superior and inferior laryngeal nerves, innervate the larynx and adjoining parts, whereas its third lateral passes to the musculature of the bronchi and larger bronchioles. It appears that the end-organs of these fibers are acted upon in a mechanical way by the distention of these tubules. Afferent impulses arise

in consequence of these impacts which are conveyed to the respiratory center, where they inhibit either the inspiratory or the expiratory movement. In this way, the expansion of the lungs gives rise to certain afferent impulses which stop this movement at a precise moment and allow expiration to set in. Likewise, the deflation of these organs incites the succeeding inspiration. This check-system is usually designated as the *self-regulation of respiration* by means of the vagus nerve.

The Co-ordination between the Respiratory and Circulatory Mechanisms.—It must be evident that the interchange of the gases in the lungs cannot satisfactorily fulfill its purpose unless a sufficient amount of non-aerated blood is constantly diverted into the pulmonary circuit. In last analysis, therefore, it will be found that it is the interchange between the blood and the cells of the tissues which must be protected above everything else; and, obviously, this interchange cannot be accomplished if the circulation is at all impaired. Accordingly, an intense ventilation of the lungs called forth by an accumulation of waste products, should invariably be associated with an increase in the rate and force of the heart beat, as well as an increased vascular tonus. These factors combined enhance internal respiration.

It is a matter of common experience that the correlation between the circulatory and respiratory mechanisms is a very close one. We well know that even a very slight muscular effort, such as is required to keep the body in the standing position, is accompanied by a greater gas exchange and hence, also by a greater cardiac and respiratory activity. Vigorous, yet not excessive, muscular exercise will increase this exchange tenfold, whereas rest and sleep will reduce it to one-half its ordinary value. All forms of exercise, when performed in a cool and relatively dry atmosphere, cause us to dissipate a larger amount of heat which must immediately be compensated for by a greater production of heat. These changes necessitate a more intense gas exchange and quickened circulation.

Breathlessness.—As is true of other mechanisms, the continued overwork of the respiratory organs finally leads

to fatigue. The symptoms associated therewith may be *objective* and *subjective, i.e.*, they may betray themselves by peculiar sensations in the respiratory muscles and parts moved by them or by a more general condition of discomfort. It is obvious, however, that they cannot be perfectly localized, because a fatigue of the respiratory muscles, exclusive of other parts, is scarcely possible under ordinary circumstances. Rated physiologically, fatigue is merely a signal set by nature against the continuance of excessive exercise and the greater activity of the cardiac and respiratory mechanisms invariably associated therewith. When this danger signal is not heeded, nature makes use of another safety appliance, namely, that of establishing *shortness of breath.* Hence, this condition may be employed as a physiological means for ascertaining the "dose" of exercise that may safely be prescribed.

Breathlessness, is merely an advanced stage of fatigue, which would finally culminate in complete dyspnœa and exhaustion. It is characterized by a feeling of distress, indicative of a failure of the gas exchange and circulation. The inspiratory movements become long and forced, whereas expiration is not materially prolonged. In order to bring this condition about in a non-fatigued animal, it is necessary to subject it to a form of exercise which will cause it to expend an unusual amount of energy in a comparatively brief period of time. But, naturally, the measure of work actually required to produce shortness of breath, differs with the state of the animal. Fatigue favors its appearance, while rest retards its onset. A simple way of producing this condition is to climb two flights of stairs in the time of one minute or four flights of stairs in two minutes. Supposing that the weight of the person is 75 Kg, and the total height of the stairs 20 m., he will have executed $75 \times 20 = 1500$ kilogrammeters of work in the course of two minutes. This work may be rated as considerable, because it corresponds to the raising of a weight of 50 kg. thirty times to the height of 1 m. In order to accomplish this amount of work an unusual degree of effort is required, and extreme effort invariably predisposes to breathlessness.

We have just noted that the respiratory requirements of the body correspond very closely to the percentage of carbon dioxid in the blood. Accordingly, breathlessness must find its cause in a superfluity of this gas in the system. Its accumulation may be explained upon the basis of either an excessive production or an impaired elimination. We well know that certain persons suffer from breathlessness even after the slightest exertion and hence, the difficulty does not seem to lie in an excessive production, but in a reduced elimination of this gas. Further, inasmuch as the ventilation ordinarily established in the lungs, is more than ample to allow for even a very considerable increase in the gas exchange, this respiratory difficulty may justly be referred to an inadequate reaction of the circulatory mechanism. This inability on the part of the heart and bloodvessels to take care of the increased respiratory activity, must lead to a passive congestion of the capillaries of the lungs and indirectly also to a diminution in the gas exchange.

It is a well known fact that persons afflicted with lesions of the valves of the heart, are made "breathless" by even very mild forms of exercise. In fact, this condition frequently arises without any exertion whatever in consequence of periodic depressions of the cardiac musculature. It is usually designated as "cardiac dyspnœa," and finds its origin in a stagnation of the blood in the pulmonary vessels and consequent lowering of the aeration of the tissues.

Breathing Exercises.—It is a matter of common experience that a person who has become "stale" from lack of exercise, cannot endure even a very moderate type of muscular effort without suffering from breathlessness. This condition, however, may be gradually overcome by physical training. Provided the person is otherwise perfectly healthy, a decided improvement should be noted from day to day as the circulatory mechanism adapts itself to the more vigorous work. A similar kind of adaptation is brought about by the process of "warming up," consisting in a brief indulgence in muscular exercise immediately before the real test is to be undertaken. The circulation is thereby put in the best possible condition for the more vigorous work that is to follow.

The discussions pertaining to the mechanics of respiration must have shown that the only safe way to increase the size and capacity of the chest, is to indulge in those moderate exercises which will require a gradually increased gas exchange. This statement implies that breathing exercises as such are insufficient and may in fact prove harmful, owing to the excessive ventilation of the lungs instituted thereby. Nature tends to prevent too copious a supply of oxygen (apnœa) and depletion of carbon dioxid (acapnia) by inhibiting the respiratory movements. Furthermore, periodic increases in the ventilation of the lungs are already provided for, because the normal person is involuntarily forced to take a deep breath at relatively short intervals. It will be seen, therefore, that the respiratory mechanism is self-regulatory, and that a greater efficiency can only be imparted to it indirectly by augmenting the gas exchange through exercise. Do not put the cart before the horse and endeavor to increase internal respiration by voluntary deep breathing without general muscular exercise.

The respiratory movements should be adjusted in such a way that all portions of the lungs are expanded in an equal measure, because it is conceivable that a continued diaphragmatic type of respiration may give rise to a poor ventilation of their apical areas. Thus, it is commonly believed that the lack of movement in the upper thorax is chiefly responsible for the fact that as many as 80 per cent. of the cases of pulmonary tuberculosis show a primary infection of the apical lobes. Exercises of support and suspension are not so well thought of as those of walking, running, and wrestling, because they tend to hinder the action of the respiratory muscles. Thus, mountaineers have large chests, because they increase their respiratory needs in the most physiological manner. They respire upon a high base-level of air with the chest always well rounded, the pulmonary vessels well distended, and the heart in a state of favorable diastolic expansion.

PART IV

NUTRITION

CHAPTER XXI

SECRETION

General Consideration.—Inasmuch as living matter is constantly called upon to yield energy, it must be placed in possession of certain chemical compounds from which it may derive this energy. Any material, the physico-chemical constitution of which may be altered by living matter so as to liberate energy, is known as a *food*. Naturally, such material may be reduced immediately upon coming in contact with the cell or may be stored in it for some time until its metabolic needs require an additional supply of fuel. Every living cell, therefore, must present two nutritive phases: namely, one during which it builds up its elementary substances, and one during which it again splits them into their simplest components and discharges them under an evolution of energy. The former process is known as *assimilation* and the latter as *dissimilation*.

These two stages, however, do not constitute the entire life history of the food, because its assimilation must be preceded by certain processes purposing to render the nutritive material available to the cell. Quite similarly, dissimilation must be followed by certain processes enabling the cell to rid itself of those substances which have been rendered useless in the course of the oxidations. These changes are most clearly revealed by the lower forms, because every free-living cell is in possession of certain means empowering it to catch the food and to digest it before it is actually assimilated. Likewise, its activities are adjusted in such a way that certain portions of its body wholly subserve the process of excretion. In many instances, however, the digestion and

excretion of the nutritive material are completed within the boundaries of a single cell, so that a division of labor is not easily apparent, although doubtlessly present.

In the higher animals, digestion is accomplished through the instrumentality of a set of specialized organs, comprising various tubular receptacles and glands. After its simplification the food is absorbed and conveyed to the cells of the different tissues to be assimilated. This process is followed by that of dissimilation, the end-products of the food being finally removed from the body by special organs, constituting the group of the excretory organs. It is to be noted, therefore, that digestion in the highest forms is extracellular in its character, because the alimentary canal in which the cleavage of the food is accomplished, lies really outside the body as far as the mass of the tissue cells is concerned. Communication is established between the source of the nutritive supply and the tissues by means of two carriers: namely, the blood and lymph.

The life-history of the food begins with its ingestion and ends with its excretion. The sum of the chemical changes taking place in it during this interim while traversing the body, is usually designated as *metabolism*, a term which really means "transformation of matter." But, since the processes of digestion take place in a membranous tube which really represents an invagination of the body-surface and lies, therefore, outside the body proper, it may not be quite correct to include ingestion, digestion and excretion under this heading. Accordingly, digestion might be more properly regarded as a pre-metabolic stage, and excretion as a post-metabolic phase. All these processes might then be classified in the following manner under the general term of nutrition:

Nutrition	Ingestion	Mastication
		Deglutition
	Digestion	Mechanical processes
		Chemical processes
	Absorption	
	Metabolism	Anabolism—cellular assimilation
		Catabolism—cellular dissimilation
	Excretion	Mechanical processes
		Chemical processes

The Purpose of Digestion.—Food is a mixture of different substances. A piece of bread or meat does not consist of a single chemical entity, but of several which are usually designated as **foodstuffs.** These foodstuffs may be arranged in the following order:

- Food-stuffs
  - Inorganic
    - Water
    - Salts
      - Chloride, Phosphate, Sulphate, Carbonate — of sodium and potassium
      - Phosphate, Carbonate — of calcium and magnesium
  - Organic
    - Proteins—nitrogenous
    - Carbohydrates, Fats — non-nitrogenous

The salts as such are not oxidized and cannot, therefore, be considered as a direct source of energy. Their chief purpose is to maintain the reaction of the fluids of the body, and to serve as tissue builders. In the absence of these salts, it would be quite impossible to form efficient media for diffusion and osmosis.

The water, salts, and simple sugars, such as the dextrose of grapes and the levulose of fruits, need not be acted upon beforehand, because they are already in so simple a form that they can traverse the lining of the intestine without cleavage. Cane-sugar, on the other hand, is not a native compound and cannot be assimilated as such, although it is soluble and diffusible. The remaining foodstuffs, inclusive of the more complex carbohydrates, must first be simplified before they can enter the absorbing channels of the body. Thus, it may be said that the purpose of digestion is to split the complex molecules of the foodstuffs into smaller ones, because only in this form are they able to pass through animal membranes, such as the mucosa of the stomach and intestine. Having reached the other side of this limiting membrane, they find their way into either the capillaries of the portal

circulation or the lacteals of the lymphatic system. Eventually they attain the general circulatory channels, and are finally assimilated by the cells of the various tissues. Hence, it may be concluded that the process of digestion strives to render the ingested material dialyzable through the limiting membranes of the body.

In order to accomplish this end, the body must be in possession of two things: namely, a receptacle in which these reductions can be brought to completion, and certain chemical substances able to institute this cleavage. The newly ingested food is forced through the different segments of the alimentary canal by the muscular action of its wall. During its passage through this membranous tube it is subjected to the action of diverse glandular products which separate its useful from its useless constituents. The chemical factor concerned with the digestion of the foodstuffs, is furnished by several glands which are either incorporated in the wall of this tubular passage or form relatively independent masses of tissue in its immediate vicinity. Each gland produces one or several active principles, possessing specific chemical influences upon the different foodstuffs. Thus, while one principle may be peculiarly adapted to split the protein molecule, another may possess a selective action upon the carbohydrates or the fats. Furthermore, the sphere of action of these agents is considerably increased by the fact that they are finely subdivided and suspended in a watery medium which allows them to form contact with very large amounts of food.

These watery media, embracing these specific digestive agents as well as a certain amount of extraneous material, are known as *secretions*. A general definition of a secretion, however, cannot be based upon its consistency, because many secretions, such as the product of the sebaceous glands, are not fluids. For this reason, it is best to define a secretion merely as a cellular product which is of further use to the body, while an excretion is a cellular product which is of no further use to the body.

Classification of the Secretions.—The general arrangement of the elements composing a secretory gland, is indicated in

Fig. 91. We observe here that a number of cells are grouped around the bulbular extremity of a small duct, their outer surfaces lying in relation with a net-work of capillaries from which the different constituents of the secretion are derived. A colony of cells of this kind is designated as an *acinus*. Many acini are combined into a *lobule*, and many lobules into a *lobe*. The gland as a whole may embrace a large number of lobes.

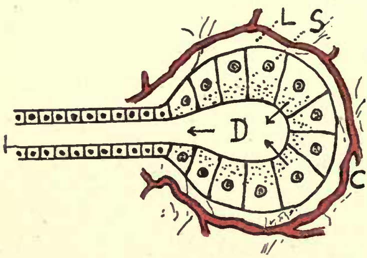


FIG. 91.—Diagrammatic representation of an acinus. *D*, duct; *S*, secretory cells; *L*, lymph space; *C*, blood capillaries.

Secretions should be classified first of all as *external* and *internal*. The "external" ones are poured upon an open surface of the body, whereas the internal ones are passed directly into the blood- or lymph-stream. The glands of external secretion are in possession of clearly differentiated membranous tubes by means of which their products are conveyed to a place situated at times at a considerable distance from them. The glands of internal secretion, on the other hand, do not possess a distinct duct. In this group belong the pineal and pituitary bodies, the thyroid and parathyroids, the thymus, pancreas, liver, suprarenal capsules, testes, and ovaries. We know that these structures furnish an important product, because their removal is followed in several of these instances by the death of the animal. Among the glands with very conspicuous ducts might be mentioned those which furnish the sweat, milk, saliva, pancreatic juice, and bile.

It is also to be noted that certain organs, such as the liver, pancreas, testes, and ovaries, produce an external as well as an internal secretion. The pancreas, for example, gives rise to the pancreatic juice which is poured into the duodenum through the duct of Wirsung and possesses a most important chemical action upon the food in this particular segment of the intestine. In addition, however, the spaces in between

the different acini of this gland contain cells of an entirely different character which furnish an internal product having to do with the metabolism of the sugars. It is a well recognized fact that the destruction of the pancreas by disease or injury and subsequent loss of the pancreatic juice, is invariably followed by a severe impairment of the digestive processes, but the most disturbing symptoms then developing are those indicating a derangement in the oxidation of the sugars. This complex of symptoms constitutes the disease of *diabetes mellitus*. Likewise, the liver furnishes an external excretion, the bile, which is concerned with the digestion of the fats, and secondly, a certain internal product which enables the cells of this organ to store the absorbed sugar in the form of glycogen.

The Active Principle of a Secretion.—The secretions with which we are most intimately concerned at this time, have to do with the cleavage of the different foodstuffs. This group of the digestive secretions includes the saliva, gastric juice, pancreatic juice, bile, and intestinal juice. All of them possess the power of simplifying the complex molecules of the food, their peculiar action being dependent upon the presence of a catalytic agent, commonly termed a *ferment*. It has been known for a long time that very minute quantities of certain substances possess the power of instigating a chemical reaction, although they themselves are not transformed nor destroyed in the course of this process. These bodies are commonly designated as ferments. The example usually cited to illustrate their action, is the splitting of sugar into carbon dioxid and alcohol under the influence of living yeast cells. Because of the "boiling up" of this solution, this process has been designated as *fermentation*, a term derived from the Latin verb: "fervere."

Experimentation, however, has proved that ferment-action does not require the presence of living cells and hence, the early classification of ferments into dead and living or unorganized and organized ferments is no longer tenable. We now know that the yeast cells may first be killed by heat and other means without destroying their power of instigating the aforesaid reaction. Accordingly, the term ferment

should be employed only in a general sense to indicate all bodies of this kind, although the term *enzyme* may be retained when reference is made to such active agents as the ptyalin of the saliva or the pepsin of the gastric juice. It should be remembered, however, that their action is the same in principle.

As has been stated above, ferments are not destroyed during the reaction incited by them and hence, the medium must still contain them after the entire process has been completed. It must be granted, however, that their recovery is not easily accomplished. It should also be noted that ferments act in very minute quantities and are specific in their nature, *i.e.*, they cannot incite several different cleavages. These agents are not contained in the cells of the gland as such but in a dormant and more elementary state. Thus, we find that the pepsin of the gastric juice is stored in the form of the inactive pepsinogen, and changes into the powerful enzyme only after it has been discharged into the duct and has been brought in contact with the hydrochloric acid of this secretion.

The fact that these enzymes do not possess a universal action, again calls to our minds the general purpose of digestion, which is to cleave the complex molecules of the food-stuffs into smaller ones. This simplification renders the otherwise useless nutrients dialyzable. Food presents a manifold appearance and composition, although always embracing one or several of the food-stuffs enumerated above. By ferment-action its useless constituents are separated from those possessing an absolute value to the body. Only the latter are rendered available for absorption by changes which, after all, are quite simple, because they consist merely in cleavages. Thus, it may be stated that enzymes are selective agents which ascertain the character of the material that should be allowed to pass into the body. In accordance with the type of the food-stuff acted upon, they are generally classified as protein-splitting or proteolytic, fat-splitting or lipolytic, and starch-splitting or amylolytic.

CHAPTER XXII

SALIVARY DIGESTION

The Alimentary Canal.—The length of the alimentary canal may be estimated at about five to six times that of the entire body. It begins above with the cavity of the mouth, and terminates below at the anus, traversing during its course the entire length of the thoracic and abdominal cavities. In the neck and thorax, it pursues a rather straight course, while in the abdominal cavity it is repeatedly wound upon itself so as to form a number of closely packed coils. The general arrangement of this musculo-membranous tube varies somewhat in different mammals in accordance with the type of the food consumed by them. Thus, the carnivorous or meat-eating animals are characterized by a short large intestine and very prominent small intestine. In the herbivora or plant-eating animals this relationship is reversed, their abdominal cavity being fully occupied by the cavernous large intestine. Man belongs to the class of the omnivorous animals which occupies in this regard a position intermediate between the groups just mentioned.

This difference in the structure of this part possesses a definite functional value, because the cleavage and absorption of the proteins are accomplished almost exclusively in the upper intestinal tract, and require only a comparatively brief period of time for their completion. The reduction of the grasses, on the other hand, often consumes several days, because their cellulose investments must first be broken up before their nutrient constituents can be attacked. The swelling, erosion, and maceration of the plants is accomplished chiefly in the beginning portion of the large intestine, the cecum. In all three groups of animals, however, the alimentary canal consists of a series of clearly differentiated segments which are known as the mouth, pharynx, œsophagus, stomach, and small and large intestines.

The Wall of the Alimentary Canal.—In general, it may be said that the wall of the alimentary tract is composed of three layers of tissue: namely, a mucous lining, an intermediate coat of muscle tissue, and an outer serous covering. These layers present the following characteristics:

(*a*) the *mucosa* is a soft, velvety lining membrane, situated upon a thin lamella of connective tissue. It contains glandular structures which secrete either a true digestive fluid or merely mucus for purposes of lubrication;

(*b*) the *muscular coat* consists of smooth muscle cells and a framework of connective tissue. These cells are arranged *circularly* around the lumen of the canal as well as *longitudinally* to it. The circular ones attach themselves in the form of a heavy layer to the mucosa. In accordance with this general arrangement, their contraction gives rise to a constriction of the lumen of the canal, while that of the more external longitudinal cells shortens this tube. The muscular movements noted along the alimentary canal are peculiar insofar as they do not consist of simple contractions of the circular fibers, but of a combined action of the two sets of muscle cells. The product of their activity is known as the *peristaltic wave*. It is to be observed that this movement presents itself as a ring-like constriction which is preceded by a band-like zone of relaxation. Both together involve the consecutive segments of the canal in the form of a wave. The food is forced ahead of the constricting area in the direction of least resistance established by the relaxation. In the stomach we also find a certain number of muscle cells which pursue an oblique course across its cardiac portion. This layer plays an important part in the process of evacuation of this organ.

(*c*) the *serous layer or peritoneum* envelops the external surfaces of the digestive tract and organs associated with it, and is finally reflected upon the internal surface of the wall of the abdomen. It appears, therefore, in the form of a visceral and parietal layer. A minute study of the course pursued by it in covering the abdominal organs cannot be undertaken at this time, although it should be noted that it forms two very important folds which are known respectively

as the *great omentum* and the *mesentery*. The former is suspended like a curtain from the greater curvature of the stomach and envelops the intestine in front in the shape of an apron. The mesentery is a duplicature which surrounds the greater part of the small intestine in the form of a sling, and fixes it more securely to the posterior wall of the abdominal cavity. Like all serous membranes, the peritoneum is moistened with a lymph-like fluid which acts as a lubricant. It is to be noted, however, that the different abdominal organs are packed closely together, so that no air is left between them. But, the alimentary canal itself often contains considerable amounts of air which have either been swallowed with the food or have been formed in the course of fermentations.

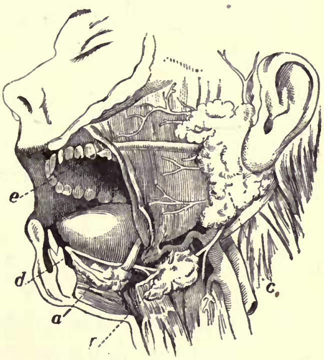


FIG. 92.—Dissection of the side of the face, showing the salivary glands. *a*, sublingual gland; *b*, submaxillary gland, with its duct opening on the floor of the mouth beneath the tongue at *d*; *c*, parotid gland and its duct, which opens on the inner side of the cheek. (*After Yeo.*)

The Changes in the Food Effected in the Mouth.—Before being ingested, the food is usually subjected to certain procedures which render it more vulnerable to the digestive juices. The process of cooking, for example, has a twofold purpose: namely, a mechanical one and a chemical one. It destroys the cellulose capsules and partitions of the vegetables, and lacerates the firm fibrous investments of the food of animal origin, such as meat. Thus, while rice and similar foods may be very completely digested (80 per cent.) without having been cooked, this procedure nevertheless aids materially in the cleavage and assimilation of their constituents. Their continued boiling disintegrates the starch granules, splitting them into an infinite number of small particles. When thus finely subdivided, they present a much larger surface to the digestive juices. Similar

15

processes are the milling of grain, and the ripening of fruits and meats.

After its entrance into the mouth the food undergoes a twofold reduction: namely, a mechanical one and a chemical one. The former process is called *mastication*. It consists in the breaking up of the larger pieces of food into smaller ones, and the subsequent amalgamation of the finely subdivided material into a rounded, softened mass which is known as the *bolus*. The chemical action taking place in this cavity is restricted to the starches and is accomplished by means of the first digestive secretion, the *saliva*. Its enzyme *ptyalin* is the active principle responsible for this cleavage.

Mastication.—The process of mastication by means of which the food is subjected to a vigorous mechanical treatment, takes place in the mouth, a chamber possessing a relatively unyielding roof but movable sides and floor. The entrance to this cavity is guarded by the *lips*, and its communication with the *pharynx* by vertically placed folds, called the *pillars of the fauces*, and a central fleshy curtain, termed the *uvula*. Both orifices are closed by muscular action, the aforesaid parts acting in the manner of bilipped valves. The roof of this cavity is formed by the *hard* and *soft palates*, its sides by the *cheeks*, and its floor by the *tongue* and adjoining soft parts, held in the solid bony frame of the mandible.

The muscles taking part in this process are arranged in such a way that the lower jaw may be either lowered or raised, moved from side to side, or protruded. Its relatively free manner of movement is made possible by the fact that the condyle of its ramus articulates with the temporal bone by means of a double condyloid joint, the capsular ligament of which is rather loose, although very strong. The raising of the lower jaw is effected by the combined contraction of the temporal, masseter, and internal pterygoid muscles, and its lowering by gravity and the contraction of the digastric, mylohyoid and geniohyoid muscles. When both external pterygoids contract, the jaw is protruded, while the activation of the internal pterygoids causes it to

recede. The contraction of only one set of these antagonistic muscles gives rise to a lateral deviation of the lower jaw in either direction.

The maceration of the material ingested is accomplished chiefly by the teeth which possess a somewhat different shape and structure in accordance with the character of the food consumed by the animal. The carnivora do not masticate very freely and rapidly project the practically unreduced pieces of food into the œsophagus and stomach, whereas the herbivora, and especially the ruminating animals, break them up into small fragments. The omnivora occupy a position intermediate between these two groups of animals. Accordingly, it is found that the teeth of the carnivora are especially adapted to catch the food, while those of the herbivora present the characteristics of grinders. It may be concluded, therefore, that the incisors of man are to hold and to divide the food, whereas the canines break it up, and the bicuspids and molars macerate it.

While the food is moved about in the mouth and finely subdivided, it is thoroughly mixed with the secretions of the different salivary and mucous glands. During this entire period the ptyalin of the saliva is able to continue its characteristic action upon the starches. Eventually the fragments of the food are again united into a soft and rounded mass, the bolus, which is then projected by muscular action into the stomach.

The Glands of the Mouth.—The lining of the oral cavity contains many *mucous glands* which furnish a watery medium in which considerable amounts of mucin are suspended. This secretion merely serves the purpose of a lubricating fluid. It should also be noted that this cavity gives lodgment to the *sublingual* and *faucial tonsils,* the former being situated below the tongue, and the latter between the pillars of the fauces. These masses of lymphoid tissue aid in the formation of small white corpuscles which are transferred from here into the lymphatic channels of the neck and thence into the venous bloodstream. It has been established that these organs do not furnish an internal secretion. Inasmuch as white blood corpuscles are greatly needed during the

early years of our life, it cannot surprise us to find that the tonsils, together with the other lymphatic glands, are usually of larger size in children than in adults. A general atrophy of these organs sets in about the twentieth year. A third organ of this character is the so-called *pharyngeal tonsil* or *adenoid* which occupies a central position upon the posterior wall of the pharynx. Owing chiefly to their exposed position, the tubular glands of these organs frequently become infected and may then serve as channels of entrance for various bacteria which finally reach the general circulation through the cervical lymphatics. Under these circumstances, as well as when these organs become so large that they seriously interfere with the passage of the respiratory air, their removal is to be strongly recommended.

The glands secreting the saliva are known as the parotid, submaxillary, and sublingual. They are paired organs. The *parotid gland* occupies the space in front of the ear, resting with its flattened inner surface upon the soft parts covering the ramus of the mandible. The membranous tube through which its secretion is conveyed into the cavity of the mouth is known as Stenson's duct. Its orifice lies opposite the second upper molar tooth, where it is recognizable as a blunt prominence or papilla upon the inner surface of the cheek. The *submaxillary gland* is situated in a groove upon the inner surface of the lower jaw, between this bone and the tongue. Its duct passes forward along the floor of the mouth and eventually opens next to the frenulum of the tongue. It is known as Wharton's duct. If the mouth is rinsed out with a few drops of diluted vinegar, drops of submaxillary saliva will be seen to ooze forth from this orifice. The *sublingual gland* lies still farther forward in the cleft between the lower jaw and the floor of the mouth. Its secretion is usually collected by a special tube which is called the duct of Ravinus.

The Minute Structure of the Salivary Glands.—The cells of the different salivary glands are arranged in groups around the dilated ends of the finest radicles of the duct. Such a group of *chief cells* constitutes an acinus. In the case of the submaxillary gland, the chief cells are limited

externally by a second type of cell which possesses a crescent shape and is known as a *demilune cell.* It should be noted first of all that the quality of the saliva closely corresponds to the general character of the gland, the most watery or serous type of secretion being furnished by the parotids, and the thickest by the sublinguals. The submaxillary glands produce an intermediate quality of saliva. For this reason, the parotids are usually designated as *albuminous glands* and the submaxillary and sublinguals, as *mucous glands.* These differences, however, are not only recognizable in variations in the stickiness or viscidity of the saliva, but also in variations in its content in solids. Obviously, the viscidity of a secretion depends upon its content in mucin, while its concentration is determined by its solids, chief among which are inorganic salts and albumin. The varying structure of these organs, therefore, leads us to infer that each gland furnishes its own peculiar type of secretion, and that a thorough mixture of them is effected only after they have been poured into the cavity of the mouth.

It is also of interest to note that these cells present certain very characteristic changes after they have been made to secrete for some time. Thus, it may easily be observed that the cells of a resting gland are large and densely loaded with granular material from which the solids of the saliva are derived. Their nuclei are irregular in outline and occupy a position near the capillary sides of the cells. When a gland is made to secrete excessively by the stimulation of its nerve, its cells grow smaller in size, while the nuclei become rounded and move into a position near the center of the cytoplasm. The dark granules which were formerly so widely distributed through the cell, are now few in number and lie chiefly in the zone nearest the duct. These changes lead us to infer that many of these granules have been transferred into the duct to become constituents of the secretion. Such structural alterations are also discernable in the cells of the pancreas and intestinal glands; in fact, they are displayed by all glands during their periods of activity.

The Innervation of the Salivary Glands.—The secretion of saliva belongs in the class of the involuntary or vegetative

functions. This statement implies that it is not under the control of the will and follows, therefore, only upon reflex stimulation. The ganglion cells controlling this action are situated in the medulla oblongata, and form a special center which is known as the *salivary center*. With the help of diverse afferent paths the activity of the latter may be varied at any time in accordance with the character of the impulses received. Its motor discharges are relayed to the glands by means of two paths, one of which pursues a direct

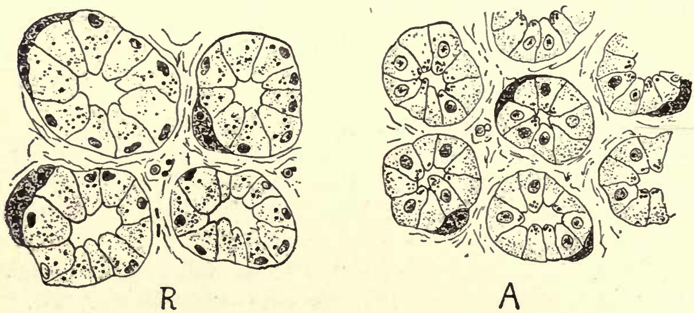


FIG. 93.—Acini of the submaxillary gland during rest (*R*) and activity (*A*). The dark outer cells represent the demilune cells.

course through the channels of the cranial nerves, and the other an indirect course through the thoracic and cervical sympathetic system. In the latter case, the path of the motor fibers has not been ascertained as yet with certainty.

It is also of interest to note that the excitation of these nerves gives rise to the formation of two very different types of saliva. Inasmuch as the same results are obtained with all three salivary glands, it may suffice to illustrate this particular point by briefly describing the changes which this procedure induces in the submaxillary gland. This organ receives its direct supply of cerebral fibers through a nerve, to which the name of *chorda tympani* has been given, because it traverses, during a part of its course, the cavity of the middle ear or tympanum. Its *sympathetic* innervation is derived from the superior cervical ganglion which forms the upper-

most station of this system. Distally to this point, these nerve fibers follow the highway of the carotid artery to the gland.

When the chorda tympani is stimulated the following changes may be noted: (*a*) the bloodvessels of this gland dilate, thereby augmenting its volume and temperature; (*b*) the flow of saliva is greatly increased; and (*c*) the saliva assumes a very watery consistency. Contrariwise, the excitation of the sympathetic fibers produces a constriction of the bloodvessels of this gland, and gives rise to the secretion of a small quantity of very thick saliva. It appears, therefore, that the cells of this gland are minute laboratories which possess a definite vital activity which in a large measure is quite independent of the bloodsupply. We shall see later that this statement may rightly be made regarding all secretory cells.

Under normal conditions the nervous mechanism controlling the secretion of saliva is activated by afferent impulses which originate either outside or inside the oral cavity. It is a matter of common experience that the smelling or seeing of food frequently suffices to evoke a copious production of this secretion. These *exherent stimuli* invariably give rise to a quick reaction and produce what is known as the psychic secretion of saliva. After the food has been placed in the mouth it stimulates the receptors of the mucous membrane of this cavity in a mechanical as well as chemical manner. These *inherent stimuli* produce a secretion which is sustained for a much longer period of time and takes the place of the quick but brief psychic flow. Obviously, the sense-organs upon which the food exerts its direct action are the taste-buds of the tongue, fauces, and cheeks.

The Character and Action of Saliva.—Saliva consists of a very large amount of water, holding in solution a small quantity of protein material, mucin, and inorganic salts. Its reaction is neutral or slightly alkaline. Its active principle is the enzyme *ptyalin* which possesses a selective action upon *starch*, changing it through several intermediary stages into *maltose*. But maltose as such cannot be absorbed until it has been further reduced into *simple sugar*. This

additional change is accomplished by the enzyme amylopsin of the pancreatic juice and a similar one contained in the intestinal juice. It will be seen, therefore, that any portion of the starch ingested that has escaped the action of the ptyalin, is not lost to the body.

The digestive power of the saliva, however, is relatively slight as may be gathered from the fact that most animals do not masticate very thoroughly, and that ptyalin is absent in many of them. Thus, while it may be said that this secretion possesses the aforesaid chemical action, its principal use seems to be rather a mechanical one, because it moistens the food and renders the mucous surfaces more slippery.

CHAPTER XXIII

GASTRIC DIGESTION

The Act of Swallowing or Deglutition.—It has been stated above that the end-product of mastication is the bolus, a rounded mass of food thoroughly moistened with saliva. In this form the food is projected into the stomach, where it is again subjected to a mechanical and chemical reduction until it has been converted into a liquid of high acidity, termed the *chyme*. The act of swallowing may be divided into three stages. The first of these is completed when the bolus reaches the aperture of the fauces; the second when it enters the upper orifice of the œsophagus; and the third, when it has passed the cardiac sphincter of the stomach.

During the first stage the oral cavity is gradually obliterated from before backward, so that the bolus is forced into the pharynx, *i.e.*, in the direction of least resistance. This act is accomplished volitionally, and although several striated muscles take part in it, the most important are those moving the tongue. This organ is raised progressively, beginning with its tip, until its upper surface has been brought in absolute contact with the hard palate. The bolus is thereby forced to escape through the aperture of the fauces. Having reached the pharynx, the bolus is grasped by the sphincters of its upper and middle segments and directed downward into the orifice of the œsophagus. At this time the posterior wall of this cavity is brought forward in close contact with the pillars of the fauces and the uvula. The bolus is now propelled through the œsophagus by peristaltic action. As has been stated above, a peristaltic wave consists essentially of a zone of constriction which is preceded by a zone of relaxation. The bolus occupies the relaxed area ahead of the constriction.

Semi-solid material requires about six seconds for its passage from the mouth to the stomach. This interval,

however, is largely taken up by its journey through the œsophagus, because this membranous tube communicates with the stomach by an orifice which is kept closed by a tonically contracted band of circular muscle fibers. As in other localities, this sphincter must first be opened by certain reflex stimuli which, in this case, appear to be wholly mechanical in nature. Fluids, on the other hand, do not elicit complete peristaltic waves, and are quickly projected into the lower segment of the œsophagus.

It is a matter of common experience that the successive acts of swallowing must be separated from one another by a definite interval, so that a sufficient time may be allowed the food to traverse the sphincter. If these intervening periods are made shorter than one second, the different motor reactions cannot be executed with sufficient precision to prevent the entrance of food into the trachea or to avoid the accumulation of an excessive amount of food above the sphincter. Such a stagnation of food usually produces severe pains in the region of the cardia of the stomach which radiate upward along the œsophagus.

Salivary digestion is usually continued for some time after the bolus has entered the cardiac end of the stomach. Obviously, since the ptyalin retains its digestive power only in a neutral or slightly alkaline medium, its action upon the starches must cease as soon as all parts of the bolus have been thoroughly moistened with the acid gastric juice. This period during which it continues its action is about 15 or 20 minutes in duration.

The Stomach.—In man the stomach appears as a single saccular enlargement of the alimentary canal. It is situated in the left hypochondriac and epigastric regions of the abdominal cavity, and extends downward to a horizontal line drawn about 2 cm. above the umbilicus. The space occupied by it varies with the state of its distention; however, even the empty organ is not fully collapsed, but contains a certain amount of frothy material. Its left extremity is very spacious, extending about 5 cm. to the left of the œsophageal orifice, while its right extremity is funnel-shaped, terminating finally somewhat to the right of the linea alba in the region

of the xiphoid cartilage. When highly distended with food, its right pole may come to lie behind the end of the cartilage of the eighth rib. Its left portion is termed the *cardia* and its right portion, the *pylorus*. The large cul-de-sac below the orifice of the œsophagus is called the *fundus*. The stomach as a whole occupies a transverse position, its long convex

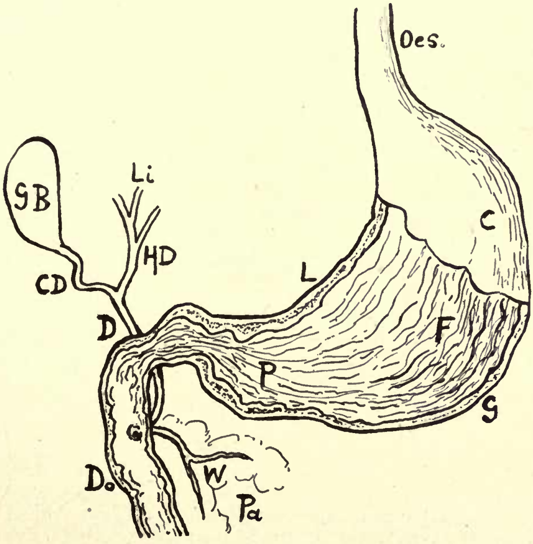


FIG. 94.—Stomach and beginning portion of intestine.
Oes., œsophagus; *C*, cardia; *F*, fundus; *P*, pylorus; *L* and *G*, lesser and greater curvatures; *D*, common bile duct; *HD*, hepatic duct; *CD*, cystic duct; *GB*, gall bladder; *Li*, liver; *Do*, duodenum; *Pa*, pancreas; and *W*, duct of Wirsung.

border or *greater curvature* being turned forward and downward, while its short concave border or *lesser curvature* is directed backward and upward.

The wall of this organ consists of a mucous lining, a middle layer of muscle tissue, and an external investing membrane of peritoneum. Its mucosa contains numerous tubular glands which secrete the gastric juice. Between these we also find a number of smaller glands which furnish a mucous fluid for purposes of lubrication. Its muscular

coat is formed by smooth muscle cells which are arranged either transversely or longitudinally to the long axis of its cavity. Upon the cardia are also found a certain number of oblique fibers which are continuous with the circular fibers of the œsophagus and terminate in its inner circular layer.

The layer of circular muscle tissue is especially conspicuous at the point where the œsophagus joins the cardia, as well as at the junction between the pylorus and the upper segment of the small intestine or duodenum. Two distinct muscular

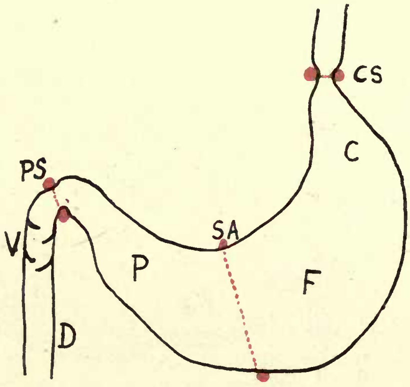


FIG. 95.—Diagrammatic representation of the stomach. *C*, cardiac end; *F*, fundus; *P*, pylorus; *D*, duodenum; *CS*, cardiac sphincter; *SA*, sphincter antri pylori; *PS*, pyloric sphincter; *V*, valvulæ conniventes.

stops are formed at these two points which are known respectively as the *cardiac* and *pyloric sphincters* of the stomach. In fact, the human stomach frequently exhibits a third band of circular fibers at the junction between the pylorus and fundus. This ring of muscle tissue is commonly designated as the *sphincter of the pyloric vestibule* or *sphincter antri pylori*. This central stop usually remains relaxed, although it may assume a constricted condition at any time in consequence of various excitations of the gastric mucosa. Such a stimulation is prone to arise when the mucosa of the pylorus has become the seat of an ulcer, or when the gastric

juice is excessively acid. In transillumination this organ then possesses the shape of an hour-glass. In this connection brief reference should be made to the stomach of the ruminating animals which consists of four consecutive compartments. It is also of interest to note that the human stomach may appear in the form of two separate organs, arranged in series, one occupying a horizontal and the other a vertical position.

The Gastric Juice.—The character of the gastric juice has been well known since about the year 1845, when Alexis St. Martin, a Canadian hunter, met with a peculiar accident which extensively lacerated his abdominal wall and adjoining portion of the stomach. In healing, a fistulous communication was established between the outside and the cavity of this organ, through which food could be introduced and again removed at a later hour to see what changes had been produced therein by the gastric juice. A number of similar cases have been reported in more recent years, because all complete obstructions of the œsophagus by growths or in consequence of erosions by corrosive liquids, are now relieved by establishing a direct communication through the walls of the abdomen and stomach. Gastric juice may also be obtained by aspirating or siphoning it through a long tube of rubber inserted through the œsophagus.

When collected from a fasting person, the gastric juice is quite clear, odorless, acid in reaction, and sour to the taste. It is secreted constantly, although in small amounts. The ingestion of food, however, calls forth a much more copious flow, amounting in dogs to as much as one liter in the course of three hours. Human beings produce about 700 c.c. of this secretion during a moderate meal. It contains three active agents: namely, hydrochloric acid, pepsin, and rennin.

The *hydrochloric acid* is derived from the chlorids of the blood. Although present only in amounts sufficient to raise the acidity of the secretion to 0.2 per cent., it destroys many of the micro-organisms swallowed with the food, and aids in the closure and opening of the cardiac and pyloric sphincters. Furthermore, on being ejected into the duodenum, it leads to the liberation of the hormone "secretin"

from the cells lining the upper intestinal tract. We shall see later that this agent stimulates the flow of the pancreatic juice, intestinal juice, and bile. The direct influence of the hydrochloric acid upon the foods consists in its establishing a suitable medium for the powerful enzyme pepsin to act in. It also aids in the erosion and destruction of the cellulose and connective tissue investments of the foods.

Pepsin is a proteolytic enzyme, and converts the proteins through several intermediary stages into *peptones*. It should be mentioned at this time that the final products of protein digestion are the *amino-acids*. The gastric juice, however, does not carry their cleavage quite so far as that, but leaves their ultimate reduction to the corresponding enzymes of the pancreatic and intestinal juices.

Rennin is a special proteolytic agent set aside for the simplification of the protein of milk, which is known as *casein*. While the relationship between this enzyme and the pepsin has not been definitely established as yet, it is obvious that it possesses a very characteristic action, consisting in the formation of the *curd*. During this change in the consistency of the milk, the protein is transferred from its soluble form or *caseinogen* into its insoluble form or casein. The casein is then reduced by the pepsin into the corresponding peptone. This reaction serves as the basis of cheese-making, the "rennet" employed to curdle the milk being obtained by scraping and extracting the mucous lining of the stomach of the calf.

The gastric juice does not possess a clearly recognizable action upon the fats. Evidently, pure fat, as is found in butter and lard, is not attacked, although emulsified fats, like cream and oil, may be reduced to some extent into glycerin and fatty acids. The enzyme responsible for this action is called *gastric lipase*. The fat of meat is imbedded in a protein framework which is destroyed by the pepsin in the presence of hydrochloric acid. The carbohydrates are not chemically altered by the gastric juice, although their capsular investments may be softened and eroded.

The Gastric Glands.—The mucous membrane of the stomach contains a very large number of tubular glands

which present the following characteristics: Their lumen is lined with large cubical and slightly granular cells which are known as *chief cells.* Outside these lie at irregular intervals numerous oval cells which are designated as *parietal cells.*

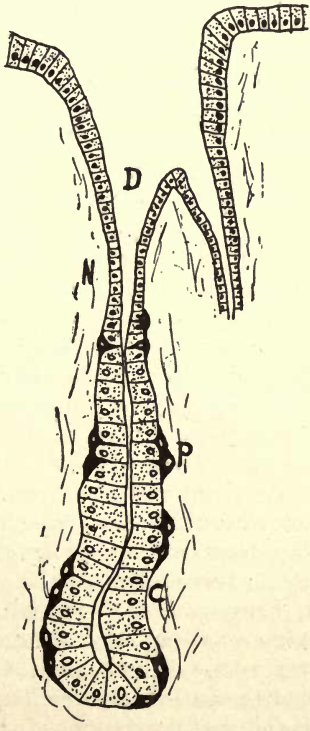


FIG. 96.—Diagrammatic representation of a fundic gland. *C*, chief cells; *P*, parietal cells; *D*, duct of gland; *N*, neck of gland.

Communication is formed between the latter and the lumen of the duct by means of delicate tubules which traverse the intercellular substance between the chief cells. Each gland is connected with the cavity of the stomach by means of a pore-like orifice.

It should be noted that the glands situated in the pyloric end of the stomach, are devoid of parietal cells, and yield a

secretion somewhat different from that furnished by the glands in the fundic portion of this organ. This difference pertains chiefly to its content in hydrochloric acid. Thus, if the stomach of a mammal is divided into two compartments, it will be found that the secretion from its pyloric pocket is alkaline, while that from its fundic portion is acid. Now, since the glands of the pylorus do not embrace parietal cells, while those of the fundus do, it may justly be concluded that these cellular units furnish the acid, while the chief cells produce the pepsin. This conclusion has recently been fully substantiated by the process of vital staining.

Inasmuch as pepsin in the presence of hydrochloric acid unfolds such powerful proteolytic properties, it may seem strange that it does not attack the wall of the stomach. It is a well known fact that erosions and ulcers of the gastric mucosa result only when the circulation has been interfered with sufficiently to evoke a disturbance in the oxidative processes of the lining cells. Furthermore, the pepsin is contained in the chief cells in the form of its inactive mother-substance pepsinogen, and develops its digestive power only after it has been cast into the acid gastric juice. Lastly, it is entirely probable that the pepsin is rendered inert when brought in contact with the lining cells. It has also been stated that the secretion of the mucous glands serves as a protective covering for these cells, but this contention cannot be substantiated, because a highly acid stomach usually contains only a very small amount of mucus and does not, as a rule, present erosions of its lining. Contrariwise, it is frequently observed that a low acid content favors the production of mucus, and that ulcerations of the gastric wall are quite common at this time.

The Secretion of Gastric Juices.—It has previously been noted that small quantities of gastric juice are secreted even during the interims between meals. Moreover, the intake of food greatly augments its flow. The stimuli giving rise to this increased secretion, may be classified as exherent and inherent. Thus, it has been proven that the gastric glands are activated some time before the food has actually entered the stomach. Certain psychic stimuli are

responsible for their activation. Consequently, the conditions met with here are very similar to those previously noted in the case of salivary secretion, because the flow of this digestive fluid follows very quickly upon the mere seeing and smelling of food. In both instances, however, this early psychic secretion is not sustained for any considerable length of time. After the food has entered the mouth and has been transferred into the stomach, it exerts a mechanical as well as chemical influence upon the lining membrane of this organ. This gives rise to a much more prolonged outpouring of gastric juice.

The mechanical stimulation consists in impacts of the semi-solid constituents of the food upon the gastric mucosa. The chemical agents present themselves in two forms: namely, as peculiar admixtures of the food which exert a stimulating influence upon the digestive processes, and as substances which arise in the stomach itself and excite its glands directly. The former are known as *vitamines*, and the latter as *secretagogues*. Gastrin is the name applied to the secretagogue liberated in this organ.

Very little is known regarding the chemical nature of the vitamines, although their presence in food has been established beyond a doubt. Such diseases as scurvy, beri-beri, pellagra, and rickets have their origin in the continuous ingestion of vitamine-free substances. Scurvy, for example, used to be prevalent upon sailing vessels when fresh meat, vegetables and fruits were unobtainable, and when fish formed the chief article of diet. In order to prevent this "deficiency disease," lime and lemon-juice were administered at intervals, because these articles contain the stimulating agents of citric acid and malic acid. Furthermore, statistics clearly prove that beri-beri has greatly increased in the East since the introduction of modern processes of milling which relieve the kernels of the grain of their capsules. Grain prepared with the capsules intact does not give rise to this disease. Polished rice is equally injurious when employed as an exclusive diet for long periods of time. The same may be said regarding pasteurized milk when fed to infants to the exclusion of other suitable foods.

It is very fortunate, however, that these metabolic disorders may be remedied without great difficulty by the administration of substances, known to be rich in vitamines. This point may be more fully illustrated by referring to those infants who have been rendered scorbutic by the exclusive feeding of pasteurized milk. When improperly executed, this manner of "purifying" the milk removes from it a certain constituent which is absolutely essential to the metabolic requirements of the infant. This constituent belongs to the group of the vitamines, but its chemical nature is wholly unknown. The alarming symptoms developed during this disease, may be remedied within a day or two by the feeding of orange juice and white of egg.

The Movements of the Stomach.—It is to be noted especially that the fundic portion of the stomach remains relatively quiescent, and serves merely as a reservoir for the pylorus. The latter is very active especially after meals. It then shows typical peristaltic movements, consisting of waves of constriction which are preceded by waves of relaxation. These movements begin at the junction between the pylorus and fundus, and slowly progress from here toward the sphincter of the pylorus. At the height of gastric digestion as many as three of these waves may be observed at any one time.

Their character and effect may best be observed by means of the Röntgen-rays after the ingestion of food containing a certain amount of subnitrate of bismuth. This salt does not permit these rays to pass, and causes the stomach to be outlined in the form of a shadow upon the barium screen. It has been stated above that the cardiac and fundic portions of this organ merely serve as a reservoir which holds the food in readiness until acted upon by the pylorus. Their contents are arranged in such a way that the material ingested most recently occupies a central position below the œsophageal orifice, while the older food is gradually forced downward and outward toward the line of junction between the fundus and pylorus. Every new wave of peristalsis developing in this region separates a relatively small mass of material from that contained in the fundus and moves it toward

the pyloric sphincter. In its downward journey it is gradually broken up into smaller pieces which, however, are not allowed to escape directly into the intestine but are again diverted toward the fundus, occupying at this time a position close to the gastric wall. These whirlpool movements of the food serve the purpose of reducing it in a mechanical way and thoroughly moistening it with the gastric juice.

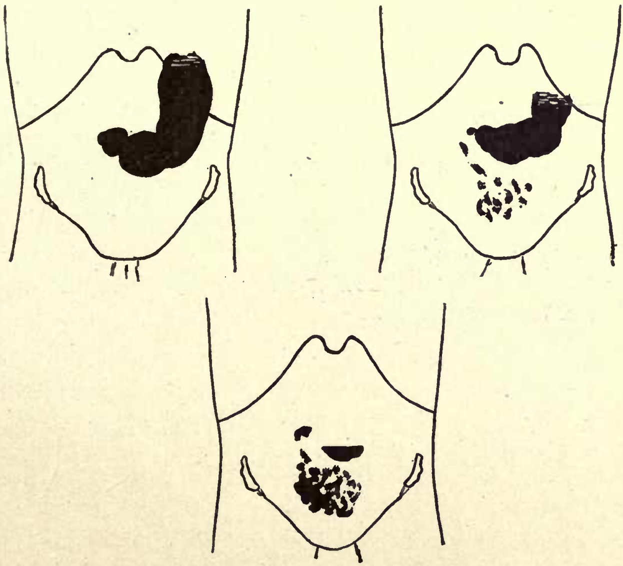


FIG. 97.—Shadows of the human stomach obtained with the aid of the Röntgen rays 15 minutes, 1 hour, and 4 hours after the ingestion of the bismuth meal.

The Evacuation of the Stomach Contents.—The time during which the food is retained in the stomach, depends upon its quantity and quality. Water and carbohydrates usually enter the duodenum within 15 to 30 minutes after their ingestion, whereas proteins and fats may require several hours for their complete reduction. This is also true of a mixed meal of ordinary bulk, because the fats always serve as retarding agents. At all events, a stomach

which does not empty itself completely within 4 or 5 hours, is not in a proper condition of tonus. It should be remembered, however, that this organ may also be prevented from emptying itself in the time specified by an obstruction at the pyloric orifice, such as may be produced by tumors and ulcers.

The ultimate purpose of gastric digestion is the formation of the chyme, a liquid of high acidity and containing practically no solid material. In this form the food is transferred into the duodenum. This process of evacuating the gastric contents embodies two distinct motor reactions: namely, certain modified contractions of the wall of the stomach and the relaxation of the sphincter of the pylorus. The cardiac and fundic portions of the stomach are then raised by the contraction of the oblique muscle fibers, while the pylorus is allowed to assume a dependent position. The peristaltic movements sweeping over the pylorus, now force the chyme through the widely opened pyloric orifice into the upper portion of the duodenum.

CHAPTER XXIV

INTESTINAL DIGESTION

The Pancreas and Its Secretion.—At a distance of about 8 cm. below the pyloric sphincter, the duodenum receives two ducts, one from the pancreas and one from the liver. The former is known as the *duct of Wirsung* and the latter

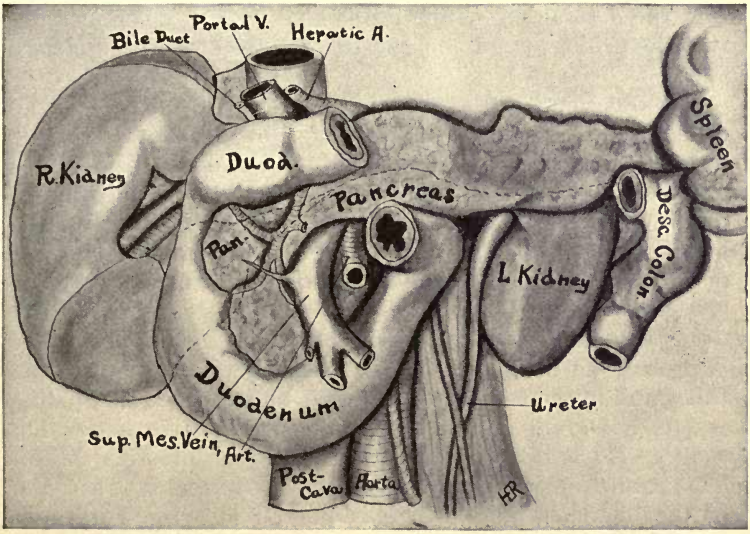


FIG. 98.—Ventral view of the duodenum, pancreas and its neighboring organs. (*Radasch.*)

as the *common bile duct*. Most generally, however, these membranous tubes are united into a single one before they actually pierce the wall of the duodenum. The pancreas is a tubulo-racemose gland, possessing a band-like shape. It consists of three portions: namely, a head, body, and

tail. Its body attaches itself closely to the duodenum, whereas its extremities lie free in the mesentery. The substance of this organ is made up of many lobules, each of which embraces a considerable number of acini, *i.e.*, groups of true secreting cells arranged around the alveoli of excretory ducts. These cells furnish the pancreatic juice. In addition, the pancreas embraces a number of cells which are not directly concerned with the formation of pancreatic juice, but furnish an internal secretion having to do with the metabolism of the carbohydrates. These cells are situated in the spaces between the different acini, forming here well defined structures which are called the *islands of Langerhans*. It will be shown later that the destruction of the latter gives rise to a complex of very disturbing symptoms, constituting the disease of *diabetes mellitus*.

The Character and Action of the Pancreatic Juice.—When collected directly from the duct of Wirsung, this secretion appears as a clear, watery fluid, containing considerable amounts of phosphates and carbonates, and especially those of sodium. Because of the presence of these salts it possesses an alkaline reaction. It also contains an appreciable amount of protein in solution, and three powerful enzymes which are usually termed trypsin, amylopsin, and steapsin.

Trypsin, the most important of the pancreatic enzymes, is proteolytic in nature. It is retained within the cells of this gland in the form of *trypsinogen*, an inactive constituent which, however, acquires its powerful digestive action as soon as it has been mixed with the general intestinal juice. This transformation is accomplished by the *enterokinase* of the duodenal juice which is poured into the intestinal canal by the *glands of Brunner*, situated directly below the pyloric orifice. While the trypsin continues the action of the pepsin, it differs from the latter in two particulars, *i.e.*, it acts only in an alkaline medium and advances the cleavage of the protein molecules beyond the stage of peptones into that of the amino-acids. These end-products are of peculiar interest, because they form protein "building stones" which are subsequently employed by the cells of the tissues in the reconstruction of their substance.

Amylopsin bears a close resemblance to the ptyalin of the saliva, because it converts starch into maltose ($C_{12}H_{22}O_{11}$), and is able to take up the work of this amylolytic agent at the dextrin stage, reducing the complex sugars into their simplest forms. It will be seen, therefore, that those complex carbohydrates which have escaped salivary digestion, are here confronted by a much more energetic amylase and diastase than the ptyalin.

Steapsin is a lipase, an enzyme specifically adapted to digest fat. Under its influence the ordinary fats are split into glycerin and fatty acids. This reduction is greatly aided by their *emulsification* in consequence of the alkalinity of this juice. Emulsification implies that the larger fat globules are broken up into a number of much smaller particles which are then subjected to the cleavage just mentioned. The process of emulsification, therefore, is really a preliminary stage in the digestion of the fats. *Saponification* then follows, because the fatty acids uniting with the alkali of the intestinal contents form soaps. In this soluble state, the fat is able to traverse the lining cells of the intestine.

The Secretion of Pancreatic Juice.—The pancreatic juice appears to be produced at intervals upon the ejection of chyme into the duodenum. The stimuli responsible for its secretion may be classified in accordance with the same general scheme as that given above in connection with the formation of the gastric juice. It is entirely probable, however, that the psychic element is of slight importance in this particular instance, and that the formation of this secretion is more closely dependent upon inherent stimuli. These local influences may be either nervous or chemical in nature. It is easily conceivable that the ejection of the acid chyme into the duodenum must evoke certain reflexes which activate the pancreatic cells. Thus, it has been noted that the flow of this juice is accurately timed, so that it takes place about two hours after the ingestion of the food until the latter is ready to leave the stomach.

The nature of this nervous reaction is not thoroughly understood. Contrariwise, a number of important data

have been gathered regarding the action of the chemical agent. Thus, it has been found that the introduction of a weak acid into the duodenum gives rise to a copious flow of pancreatic juice, and, peculiarly enough, this result is also obtained after the nerves innervating the pancreas have been cut. Secondly, it has been noted that the injection into the bloodstream of an extract of the lining membrane of the duodenum evokes a copious secretion of this juice. Accordingly, it has been concluded that the entrance of the acid chyme into the duodenum liberates a secretagogue which reaches the pancreas through the circulation and acts as a direct stimulant to its cells. This secretagogue is retained in the duodenal mucosa in a dormant form and requires the chyme for its normal activation. The name of *secretin* has been applied to it. Like gastrin, this chemical stimulant of secretion belongs to the group of the hormones, peculiar products of cellular activity which exert a chemical influence upon different functions of our body.

The Liver.—The liver is the largest glandular organ in the body. It weighs about 1400 to 1700 grams (50 to 60 ounces), and measures 25 to 30 cm. (10 to 12 inches) from side to side, 15 to 17 cm. (6 to 7 inches) in breadth, and about 7 cm. (3 inches) in thickness. It occupies the right hypochondriac and epigastric regions. Its upper convex surface lies in immediate relation with the diaphragm, while its lower surface touches the pyloric end of the stomach, duodenum, hepatic flexure of the colon, and right kidney. The entire organ is divided by five grooves into a corresponding number of lobes, of which the right is much larger than the left. Externally, this organ is enveloped by a layer of connective tissue, forming a distinct capsule. Connective tissue sheaths and septa enter its interior, subdividing its mass into numerous smaller segments or lobules.

The individual lobules of this organ measure about 2 mm. in diameter and are composed of a large number of many-sided, nucleated and granular cells which are invested by an intricate network of capillaries. The arrangement of the latter will be more easily understood, if it is remembered that the liver receives its bloodsupply from two sources:

namely, from the *hepatic artery* and the *portal vein*. The former is a branch of the cœliac axis and conveys the blood of the abdominal aorta directly to this organ, nourishing its framework but not contributing materially to its store in secretory material. As has been mentioned in one of the preceding chapters, the portal vein serves as the common collecting channel for the group of the portal organs, which

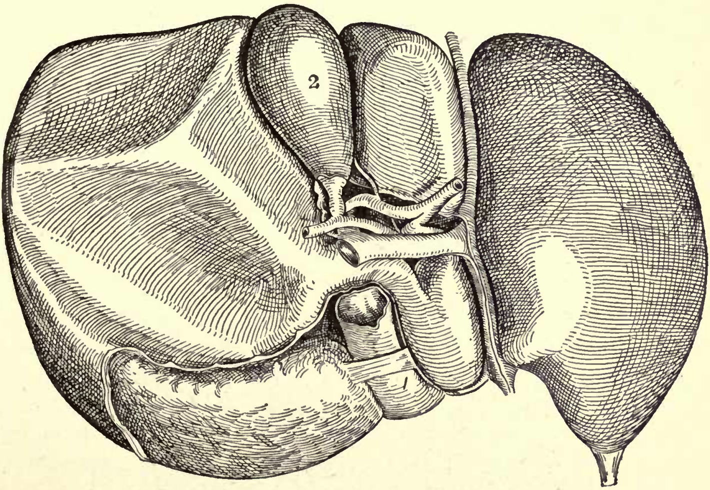


FIG. 99.—The liver, seen from below. 1, inferior vena cava; 2, gall bladder. (*Morrow.*)

embraces the stomach, intestine, pancreas, and spleen. This large venous tube enters the hilum of the liver, where it divides into a number of smaller channels, and eventually into an intricate system of capillaries. These minute tubules also receive the venous drainage from the hepatic artery, but this type of blood does not serve as an important source of secretory material under normal circumstances.

As is indicated in Fig. 100, the portal terminals form a ring-like plexus of small vessels around the periphery of each lobule, whence the true capillaries strive radially toward its center. The *hepatic cells* lie closely packed in the spaces between these capillaries. The venous collecting channel

of each lobule, or *intralobular vein,* unites with others to form the *hepatic vein* which eventually pours its contents into the inferior vena cava. It need scarcely be emphasized that the function of the liver resides in the hepatic cells which derive their secretory material chiefly from the portal bloodstream.

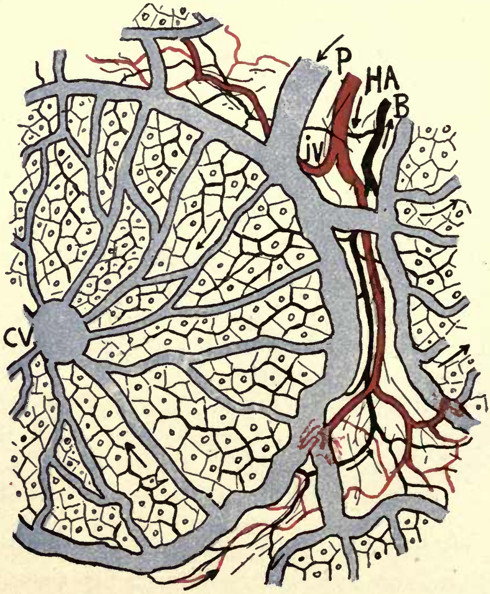


FIG. 100.—Diagrammatic representation of the blood supply of the liver acini. *P*, portal terminal; *JV*, interlobular veins; *CV*, central veins which are eventually collected in the hepatic vein; *HA*, hepatic arteriole, the interlobular capillaries of which empty into the portal terminals; *B*, biliary capillary which begins as biliary space between the hepatic cells.

The Functions of the Liver.—While we are now mainly concerned with the digestive secretion of the liver, it seems advantageous to amplify this discussion by briefly summarizing all the important functions of this organ. Inasmuch as the liver lies directly in the path of the portal blood which is heavily laden with the products of intestinal digestion, it

need not surprise us to find that it exerts a most powerful influence upon all the metabolic functions of the body. Of principal importance to us at this time are the data which prove that this organ:

(*a*) Furnishes an internal secretory product which plays an important part in the metabolism of the carbohydrates, because it converts the sugar of the portal blood into *glycogen*. In this form the sugar is stored in the hepatic cells until needed by the cells of the different tissues. At this time the glycogen is reconverted into simple circulating sugar;

(*b*) Forms those bodies of protein cleavage which are later on excreted by the kidneys in the form of urea;

(*c*) Contains certain cellular elements by which the red blood corpuscles are destroyed;

(*d*) Plays an important part in the coagulation of the blood, because it gives rise to certain bodies which retard this process;

(*e*) Forms an important external secretion, the bile, which aids in the cleavage of the fats; and

(*f*) Conserves the body-temperature, because it produces a considerable amount of heat and protects the large abdominal vessels against an undue loss of heat.

The bile is a slightly alkaline fluid, of decidedly bitter taste and high degree of viscidity. It possesses a golden yellow color in the carnivora and a greenish color in the herbivora. Its appearance, however, changes very quickly on exposure, because its pigments are easily oxidized. The biliary coloring material of the carnivora is called *bilirubin* and that of the herbivora, *biliverdin*. In addition to these constituents the secretion also embraces certain compounds of sodium with organic acids which are called *bile-salts*, as well as a number of inorganic salts and cholesterin. It is to be noted especially that the bile contained in the smaller biliary passages is very watery, while that in the outer channels and gall-bladder is very viscid. The substance chiefly responsible for this change in its consistency is *mucin*, a product of the cells lining the larger ducts and gall-bladder. Owing to its peculiar physical properties, this admixture

serves to retard the progress of the food through the intestine, so that a more thorough separation of the nutritive substances may be effected. Secondly, the mucin serves as a protective and lubricating agent for the lining cells of the intestine.

The digestive function of bile is relatively unimportant, because it does not contain an enzyme; however, since it is alkaline in its reaction, it must aid in the emulsification and saponification of the fats. In this regard, therefore, it may be considered as an adjunct to the pancreatic juice. It is stated further that it possesses very decided antiseptic properties, but this action seems to be brought about in an indirect way, because it exerts a marked stimulating influence upon intestinal peristalsis. Inasmuch as an increased peristalsis hastens the onward movement and discharge of the fæces, the bacteria inhabiting the intestinal canal cannot multiply so profusely as when the progress of the fæcal material is slow. This fact is clearly proven by the changed character of the intestinal contents, following those lesions of the liver and its excretory ducts which cause a stoppage in the inflow of bile. The fæces then become very sticky and odoriferous, while their color gradually changes to gray. These alterations are easily explained, because in the absence of bile, a large portion of the fats remains undigested, while, owing to the diminished peristalsis, the processes of putrefaction may continue for a much longer time than is usual. The change in color is due, of course, to the loss of the biliary pigments.

The Storage of Bile.—The bile is secreted constantly, although it is not allowed to pass into the duodenum in a steady stream. It will be noted that the *hepatic duct* unites at some distance from the hilum of the liver with the *cystic duct* to form the *common bile duct*. As has been stated above, the latter opens into the duodenum in conjunction with the duct of Wirsung of the pancreas. It is to be observed that the orifice of the common bile duct is guarded by a sphincter which is kept closed until the chyme has been ejected into the duodenum. Consequently, since the bile emerging from the hepatic duct cannot enter the intestine, it must

back up through the cystic duct into the *gall-bladder.* Thus, it may be said that this musculo-membranous pouch serves as a reservoir in which the bile is stored until needed in the duodenum. (Fig. 94) After the ejection of the gastric contents, however, the sphincter of the common duct relaxes, and allows the contracting gall-bladder to evacuate a portion of its bile. The reflexes responsible for this motor action, are elicited in a nervous way.

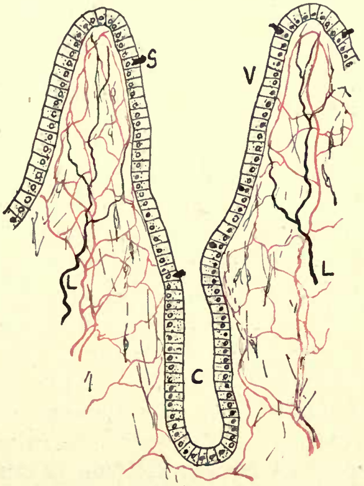


Fig. 101.—Diagram to illustrate the relation between the villi and the crypts of Lieberkühn. *V*, villus; *G*, goblet cells secreting mucus; *C*, crypt of Lieberkühn; *L*, lacteal.

It might also be mentioned that certain animals, such as the horse, are not in possession of a gall-bladder and hence, show a relatively constant influx of bile into the duodenum. This appears to be an absolute necessity in these animals, because their digestive activities are never at a complete standstill. The presence of the gall-bladder, however, is not a functional necessity even in man, because those persons from whom this organ has been removed to remedy a certain abnormal condition, do not present any permanent disturbances. It is entirely probable that the larger bile ducts then

assume the function of a reservoir. Brief reference should also be made at this time to those conditions which lead to a stagnation of the bile in the gall-bladder and biliary passages. These effects are most frequently caused by the impaction of gall-stones or mucous plugs in the large biliary channels. The steadily increasing stagnation of the bile eventually allows the coloring material of this secretion to pass into the lymphatics, whence it reaches the general circulatory system. It is then deposited in the different tissues, imparting to them a yellowish color. This condition is known as *jaundice* or *icterus*.

The Intestinal Juice.—The mucous lining of the small intestine contains a large number of tubular glands which are situated in the depressions between the neighboring villi. They are known as the *glands of Lieberkühn*. While these structures are also present in the large intestine, they assume here a more superficial position, because the mucosa of this segment of the alimentary canal is free from villi. Furthermore, their secretion no longer possesses a true digestive action, but merely serves, by virtue of its large content in mucin, as a protective and lubricating fluid.

Each gland of Lieberkühn is lined with a layer of cubical cells, somewhat different in their general appearance from those limiting the villi. The secretion furnished by these cells contains several ferments. One of these, known as *erepsin*, is proteolytic in nature, while its *invertase* and *maltase* act upon the complex sugars changing them into glucose.

CHAPTER XXV

THE PROGRESS OF THE FOOD THROUGH THE INTESTINES—ABSORPTION

Movements of the Small Intestine.—The movements taking place in the small intestine are of two kinds: namely, *pendular* and *peristaltic*. Very soon after the chyme has been ejected into the duodenum, it is subjected to a minute subdivision by the smooth musculature of this particular portion of the alimentary canal. This action consists in an alternate constriction and relaxation of its consecutive

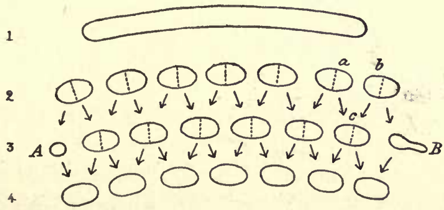


FIG. 102.—Diagram to show the effect of the rhythmical constricting movements of the small intestine upon the contained food A string of food (1) is divided suddenly into a series of segments (2); each of the latter is again divided and the process is repeated a number of times (3 and 4). Eventually a peristaltic wave sweeps these segments forward a certain distance and gathers them again into a long string, as in (1). The process of segmentation is then repeated as described above. (*Cannon.*)

segments. Thus, while one of its band-like portions passes into the state of contraction, the one nearest to it remains perfectly flaccid. A moment thereafter, however, the previously constricted segment relaxes, while the flaccid one contracts. The adjective "pendular" has been applied to this movement, because it swings back and forth from loop to loop like the pendulum of a clock. It has also been

characterized as rhythmic, because it recurs at rather regular intervals.

As a result of this alternate constriction and relaxation, the larger masses of food are constantly broken up into smaller pieces and thoroughly moistened with the intestinal juices (Fig. 102). Later on, when the intensity of this movement diminishes, the smaller portions are again united into a single one. This rebuilt mass of nutritive material is then moved onward by waves of peristalsis, pursuing a course from above downward. At a somewhat lower level of the small intestine it is again subjected to this rhythmic segmentation, and so on until the distal portion of the ileum has been reached. The peristaltic waves occurring in the small intestine, always pass from above downward, and may involve either a short or a long segment of this gut. This form of movement is known as *regular peristalsis.* Waves moving in the opposite direction are not observed in the small intestine under normal circumstances, although they may arise in consequence of obstructions to the fæcal material by tumors and adhesions.

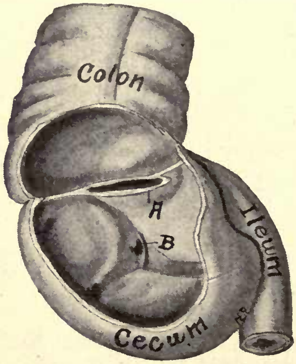


FIG. 103.—Cæcum with part of the ventral wall removed. *A*, ileocæcal valve and orifice; *B*, appendicular orifice. (*Radasch.*)

Movements of the Large Intestine.—The movements discernible in the large intestine present the same general characteristics as those occurring in the small intestine. It is to be emphasized, however, that the *anti-peristaltic motions*, consisting of waves progressing in a direction from below upward, are here more conspicuous than the regular ones. Even a casual observation will show that this portion of the alimentary canal is not equally active throughout, for while the cæcum and ascending colon show an almost constant peristalsis, the transverse and descending colons are relatively quiescent. When the contents of the ileum escape through

the ileo-cæcal orifice into the cæcum, they are still in a fluid condition. Their content in water, however, is greatly diminished during their passage through this gut, so that they reach the transverse colon in a much more solid state.

This absorption of water is greatly facilitated by the fact that the fæcal material is not allowed to pass right on, but is moved forward and backward repeatedly without being able to gain the transverse colon. After its entrance into the cæcum, it is grasped by regular peristaltic waves and moved upward into the hepatic flexure. Here it meets with waves pursuing an opposite course, and is again carried into the pit of the cæcum. This movement is repeated many times until relatively water-free portions of this material finally succeed in passing over into the transverse colon.

The transverse portion of the colon serves chiefly as a storehouse for the fæces. Here they accumulate throughout the day, and are eventually removed from it by regular peristaltic waves which force them through the descending colon into the rectum. As a rule, these movements are few in number and occur during the early hours of the morning, when the entire system after its long period of rest, is most sensitive to mechanical impacts and the effects of gravity. As this material accumulates in the rectum, it exerts a mechanical influence upon the mucous lining of this part in consequence of which certain reflexes are evoked giving rise to the act of defecation. This process consists of two simultaneous muscular reactions: namely, the relaxation of the internal and external sphincters guarding the orifice of the rectum, and the contraction of the smooth muscle cells situated in its wall. The expulsion of the fæces may be considerably hastened by the contraction of the muscles of the abdominal wall, provided the glottis is kept closed. If these reflexes are antagonized by volition, they may lose their normal intensity and presently fail to develop altogether. The rectum then becomes highly distended with fæcal material without giving the sensations of fullness and discomfort. Further, the repeated volitional interference with these reflexes generally results in a disturbance in the

function of this mechanism which can only be remedied with difficulty.

The Progress of the Food Through The Intestines.—It has been stated above that the contents of the stomach are evacuated at intervals, and that a normal organ should

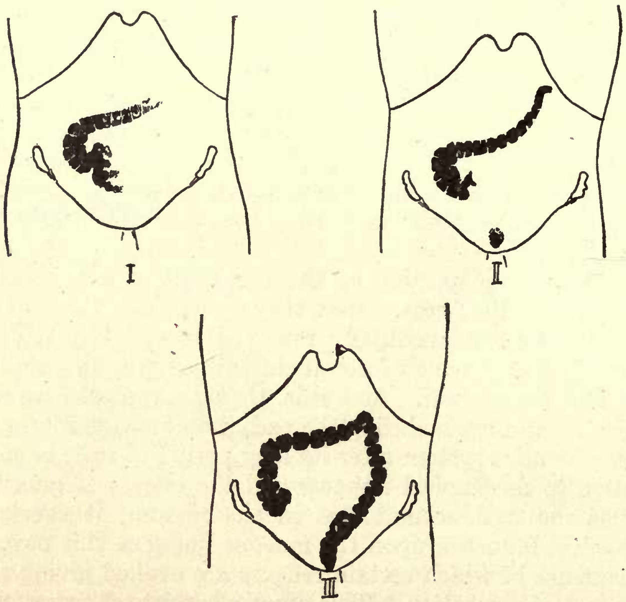


Fig. 104.—Shadows of the human large intestine obtained by means of the Röntgen rays. I, Entrance of the contents of the ileum into the cecum and colon. II, the material has progressed through the transverse colon as far as the splenic flexure, some has escaped into rectum. III, the large intestine outlined by means of a solution of sub-nitrate of bismuth injected through the rectum.

empty itself in less than five hours after the ingestion of a mixed meal of ordinary bulk. The small intestine is traversed in about five hours, although this portion of the alimentary canal is about 25 feet in length. Markedly different conditions are met with in the large intestine, because while this segment is only about 6 feet in length, the food requires almost 20 hours in its journey to the rectum. It has been

mentioned above that this entire mechanism is adjusted in such a way that the food consumed in the course of the preceding day, is evacuated during the early hours of the following morning. It is true, however, that exceptions to this rule are not uncommon, and are due to differences in the character of the food and the functional power of the intestine as well as of that of the entire body.

The Formation of the Fæces.—The function of the small intestine is to separate the useful from the useless constituents of the food. The former are immediately transferred into the absorbing channels of the body, while the latter are allowed to escape through the ileo-cæcal orifice into the large intestine to be eventually included in the fæces. Almost every food contains a certain amount of indigestible material which is made up chiefly of the cellulose of the walls of the plants and the dense fibrous constituents of connective tissue. In addition, the large intestine receives that portion of the proteins, carbohydrates and fats which has escaped digestion, as well as a certain amount of excretory material derived principally from the bile. The fæces also contain enormous numbers of bacteria, living as well as dead, and in addition a few lining cells that have been torn loose from the mucosa.

Under normal conditions, however, only about 5 to 10 per cent. of the food ingested is allowed to escape into the large intestine, where it is subjected to fermentative changes yielding a small proportion of absorbable material. This is taken up before it actually reaches the transverse colon. Even the cellulose may be decomposed to some extent by bacterial action, allowing the proteins and carbohydrates to become separated from their capsular investments and to be chemically reduced by fermentation. In the herbivora, somewhat different conditions are met with, because their food consists chiefly of cellulose material, in the meshes of which different nutritive substances are contained. Thus, it will be noted that the beginning portion of the large intestine of these animals is often excessively distended with grasses and leaves undergoing prolonged fermentative changes before they are actually passed on.

The conditions in the lower bowel are well adapted to bacterial life and growth. The products derived from their action upon the remnants of the food are in most instances perfectly harmless. Nevertheless, it cannot be denied that several of them are capable of evoking certain disturbing general symptoms, such as dizziness, muscular tremors, headache, and fatigue. The most poisonous of these compounds find their origin in the decomposition and putrefaction of the proteins. In remedying this difficulty, it should be our endeavor to increase the peristaltic activity of the intestines, so that the bacteria cannot multiply so rapidly. Naturally, the intake of protein foods should be reduced to a minimum. It must be evident that the administration of a cathartic can afford only temporary relief, because the quick evacuation of the fæces does not necessarily produce a permanent augmentation of the tonus of the intestinal musculature. This end can only be attained by general hygienic measures.

Absorption.—The term absorption refers to the passage of the simplified foodstuffs through the lining cells of the alimentary canal. These cells form an animal membrane, separating the contents of the digestive tract from the general fluids of the body. Accordingly, this subject-matter is chiefly concerned with the processes which enable the products of digestion to reach the two absorbing channels of the body: namely, the capillaries of the portal system and the lacteals. The principal organ of absorption is the small intestine, but certain substances, such as sugar and peptones, may also traverse the lining of the stomach as well as that of the colon. In general, however, it may be stated that the absorption of the simplified foodstuffs has been completed by the time the ileo-cæcal orifice is reached. Even water follows this path, and only a relatively small proportion of it escapes into the large intestine. Practically none is absorbed in the stomach. The inorganic salts behave in the same way as water.

The foregoing discussion pertaining to the cleavage of the different foodstuffs, must have shown that the lumen of the small intestine contains: (*a*) simple sugars derived from the various carbohydrates; (*b*) amino-acids, as products of

protein digestion; and (*c*) emulsified and saponified fats. In these forms the various foodstuffs are able to traverse the intestinal wall and to enter the absorbing channels. Curiously enough, by far the largest amount of the fat absorbed selects the lacteals as its specific channel of entry. It has been mentioned above that the lymph then assumes the character of an oil emulsion and becomes milky in appearance. Lymph loaded with these minute globules of fat is called chyle. At this time, even the blood presents an oily appearance, which is due to the steady inflow of chyle from the thoracic duct. It will be remembered that this channel collects the lymph from all the lacteals, and conveys it directly into the blood of the left subclavian vein. The sugars and amino-acids are conveyed into the blood-capillaries of the intestine, whence they reach the liver by way of the portal vein and its terminal branches.

The Intestinal Lining Cells as Factors in Absorption.—The mucous membrane of the intestine is composed of innumerable cells arranged side by side. Their outer surfaces lie in relation with the digested foodstuffs, whereas their inner surfaces border upon the body-fluids, the blood and lymph. These cells, therefore, form a living membrane, through which the products of digestion must pass in order to reach the circulatory channels of the body. In its normal state this membrane is *semi-permeable, i.e.*, it allows certain substances to pass and not others. It will be evident that the other two types of membranes: namely, the *permeable* and *impermeable* ones, need not be considered in this connection, because the former permit the passage not only of water, but also of the substances dissolved therein, while the latter are completely impervious to both.

The question may then be asked, whether these lining cells exert a vital selective action upon the substances contained in the intestinal canal, or simply permit them to traverse their cytoplasm in accordance with ordinary physical laws. It seems proper for us to take a more conservative view than either, and to state that while the laws of pressure, diffusion and osmosis play an important part in absorption, several of the phenomena connected with this process cannot

be fully explained upon this simple mechanistic basis. Consequently, it may be assumed that these lining cells play the part of minute laboratories and are able to force the nutritive substances through their cytoplasm in an active way, modifying them in their passage in such a way that they become available for tissue metabolism. The nature of the chemico-physical processes occurring within these cells, is not clearly understood as yet and hence, it seems permissible to designate them by the general term of *vital activity* or *vitalismus*. Accordingly, it may be concluded that the absorption of the foodstuffs depends upon differences in pressure, diffusion and osmosis, as well as upon certain inherent physical and chemical powers of these lining cells.

In harmony with the preceding statement, the lining cells of the intestines may be compared to glands with this difference, however, that they secrete from without inward. They select various substances from the contents of the intestinal canal and transfer them eventually into the absorbing channels. In several instances, this transfer is associated with true constructive changes. The simple products of digestion are rebuilt into complex compounds akin to those found in the different tissues of the body. This is true especially of the fats, the glycerin and acids of which are reconstructed during their journey through the intestinal mucosa into a form practically identical with that of the neutral fats of the body. In other words, these cells are able to synthetize the products of the cleavage of this foodstuff. The nature of this synthesis is as yet unknown.

Diffusion, Osmosis, Dialysis.—The passage of water and salts may be explained in accordance with the ordinary physical laws of diffusion and osmosis. If a solution of a salt is placed in a receptacle and a layer of water is allowed to run over it, it will be found after a time that a certain number of molecules of the salt have passed into the overlying water, thereby establishing a medium of uniform composition. Such an interchange also takes place if two solutions of different salts are brought in relation with one another. This spreading about or scattering of the molecules through suitable media is termed *diffusion*.

If we now interpose a semi-permeable membrane between the salt solution and the water, the molecules of the water will gradually pass through the pores of this septum into the solution, raising the level of the latter. This movement of water from one side of the membrane to the other in response to differences in the molecular concentration of the fluids is known as *osmosis.* It may be illustrated by filling a thistle tube with a solution of magnesium sulphate; closing its orifice with an animal membrane, and immersing the entire cup in water so that the level of the latter corresponds precisely with that of the salt solution. This contrivance is known as an *osmometer.* After several hours it will be found that the salt solution in the thistle tube has risen to a considerable height, proving thereby that an appreciable back pressure has been established against the membrane. This pressure, which is termed *osmotic pressure,* is responsible for the inflow of the molecules of water. When magnesium sulphate or epsom salt is used as a cathartic, it causes a transfer of water into the intestinal canal, thereby rendering the fæces more fluid.

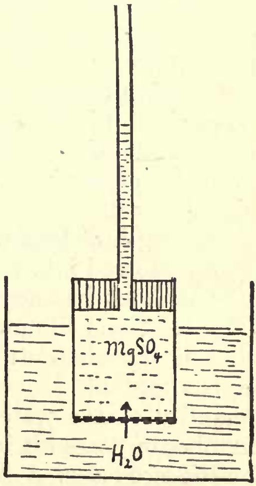


FIG. 105.—A simple osmometer. The receptacle contains water, and the cell a solution of magnesium sulphate. As the molecules of water are drawn through the semi-permeable membrane, the level of the solution rises.

The manner in which the osmotic pressure is produced may be illustrated in the following way: Supposing that we fill an elastic membranous ball with a solution of cane sugar and immerse it in water. If the wall of this ball is equipped with many minute pores which are sufficiently large to allow the molecules of water to pass but too small to permit the escape of those of cane sugar, the ball will eventually become highly distended. Obviously, this distention indicates that the fluid within has been placed under a

high pressure. How does it happen that although these pores allow the passage of the molecules of water in both directions, the number of these molecules is constantly increased on the inside of the membrane? Inasmuch as the ball is filled with a solution of cane sugar, the number of the molecules of water present therein must be smaller than that in an equally large volume of clear water. Secondly, since the molecules of cane sugar constantly hit the pores but cannot get through, they must prevent each time the passage outward of a molecule of water. Contrariwise, no hindrance is placed in the path of the molecules of water upon the outside of the membrane.

This process may easily be reversed by placing the ball containing the aforesaid solution, in a solution of twice the strength of that within it.. The molecules of water will then be forced into the outside compartment until the solution without has acquired the same concentration as that within. The ball now decreases in size. It will also be seen that if the concentration of the solution within the ball equals that of the surrounding medium, no change in the quantity of the water within can take place, because the number of pores hit by the sugar molecules is now the same on the two sides.

A solution possessing the same concentration and osmotic pressure as the blood plasma, is said to be *isotonic*. Contrariwise, one showing a greater osmotic pressure is characterized as *hypertonic*, and one possessing a lesser osmotic pressure as *hypotonic*. While many such simple arrangements actually exist in our body, the most frequent interchanges are those affecting the crystalloids and colloids. The process of interchanging these complex substances in both directions through an animal membrane is known as *dialysis*.

CHAPTER XXVI

METABOLISM

The Life History of the Carbohydrates.—While animal foods are poor in carbohydrates and rich in proteins, vegetables usually contain copious amounts of carbohydrates, and especially of starch. This starch is generally contained within the plant cells, the walls of which are composed of cellulose membranes, impermeable to the digestive juices. For this reason, plant foods such as cereals, vegetables, fruits and nuts, must first be separated as much as possible from their indigestible investments by the process of threshing in the cases of rye, barley, wheat, and oats, and by the processes of shelling, husking, and peeling in the cases of corn, nuts, potatoes, celery, radishes, and similar nutritive bodies. These procedures having been completed, these foods are subjected to further refining by winnowing, grinding, cleaning, and cooking. The purpose of the separation of the useless from the useful materials is to concentrate the food before it is actually subjected to the process of digestion. In principle, however, the purpose of the "internal" refining of the food is the same as that of the "external," because it continues the processes already started in the field, mill and kitchen, finally cleaving the concentrated foodstuffs into their simplest components.

The large molecules of starch are first acted upon by the ptyalin of the saliva. Maltose is the result of this cleavage. Together with the simple sugars, the maltose then traverses the stomach unchanged by the gastric juice, and is again acted upon by the amylopsin of the pancreatic juice as well 3
as by the invertase of the intestinal secretion. Dextrose, glucose and other sugars of the simplest order are the result of this series of digestive events. Chief among these is dextrose which appears to be practically identical with the sugar found in grapes.

It will be remembered that the green parts of the plants, and especially the leaves, manufacture sugar from the carbon dioxid of the air and the water of the soil, the energy required for this reaction being furnished by the sunlight. This sugar solution is transported from cell to cell in the form of the sap and serves as a source of energy to the plant. The excess of sugar is converted into starch and is stored in the form of granules in the cytoplasm of the different cells. This stored energy serves as reserve fuel and is drawn upon whenever the plant is not able to form fresh sugar. At this time the starch is reconverted into sugar.

Let us see whether we cannot discover a certain similarity between this process and that taking place after the simple sugars have traversed the intestinal lining cells and have entered the bloodstream. Sugar serves as an important fuel for our tissues, especially the muscle cells. It is a well known fact that every contraction of muscle uses up a certain amount of this substance, and hence, it may be conjectured that the body must always be well supplied with it. Accordingly, it is found that the sugar conveyed to the liver by the portal blood stream, is stored in the cells of this organ for future use. Whenever the body is in need of extra amounts of sugar, this starch-like body glycogen is reconverted into simple circulating sugar and oxidized.

The carbohydrate material which is stored in the cells of the liver, is known as animal starch or *glycogen*. It is more like a starch than a sugar and exhibits, therefore, a limited solubility and high molecular weight. It is found in the aforesaid cells in the form of delicate chips and its presence is directly demonstrable by chemical means. It appears, therefore, that a portion of the simple sugars of the portal blood is condensed or dehydrated into a stationary form, but may at any time thereafter be reconverted into its original condition. Accordingly, the formation of glycogen is accomplished by a process the reverse of that leading to the cleavage of the starch and complex sugars. It is usually stated that the liver cells accomplish this change by means of an internal product or secretion, the nature of which is unknown.

A storage of sugar also takes place in other tissues, prin-

cipally the skeletal muscles. Hence, the liver should be regarded merely as a central store house, from which the other reservoirs are supplied whenever their content in glycogen has been depleted. It is to be noted, however, that while the percentage of sugar in the muscles is small, their total sugar content must be considerable, because the entire mass of muscle tissue is very much larger than that of the liver. All the tissues together store probably as much as 1 lb. of glycogen. The final product of the oxidation of sugar is carbon dioxid and water.

Impaired Carbohydrate Metabolism.—Because of the constant oxidation of the circulatory sugar by the tissues and the storage of the superfluous amounts of this foodstuff in the form of glycogen, the blood is not able to retain a significant amount of it. Furthermore, owing to the aforesaid means of balancing the ingo and outgo of sugar, its percentage in the blood must remain practically constant. But if the ingo of sugar greatly exceeds its outgo and an ample amount of glycogen has been deposited in the tissues, the body may change its excess quantity into fat. This "carbohydrate-fat" differs somewhat from the ordinary tissue-fat which is usually derived from the fat of the food and in a small measure also from the excess proteins. This power of the body enabling it to form tissue-fat from other foodstuffs, explains the fact that the consumption of excessive amounts of carbohydrates is prone to lead to corpulence and adiposity. This condition is common in heavy drinkers of beer and malt extracts, but, naturally, the alcohol may play an important part in the deposition of excessive amounts of fat, because it is easily oxidized into carbon dioxid and water and protects, therefore, the carbohydrates and fats. The latter are thereby spared and may be stored directly. Alcohol as such, however, is not a food. Its nutritive value is entirely due to an indirect cause.

It has been mentioned above that the pancreas furnishes not only an external secretion, but also an internal one which is concerned with the metabolism of the carbohydrates. This internal product arises in the cells of the islands of Langerhans, and possesses a peculiar influence upon the constitution

of the circulating sugar. It changes this substance into a form which can be easily oxidized by the tissue cells. Not having been subjected to this modification, the sugar cannot be utilized completely by the cells, and must then accumulate in the blood and eventually escape into the urine.

This lack of pancreatic hormone and resulting inability on the part of the tissue cells to reduce the sugar, finally give rise to a complex of symptoms characterizing the condition of *diabetes mellitus*. As is evident from the foregoing discussion, this disease is metabolic in its nature and is not due to a derangement of kidney function. It is only natural to suppose that the accumulation of sugar in the blood must finally force the kidneys to eliminate this substance in an attempt to keep the concentration of the blood at its normal low level. It should be noted, however, that the urine always contains slight amounts of sugar and albumin, and hence, a distinctly abnormal condition can only arise when its content in these substances exceeds a certain low limit. Furthermore, sugar invariably escapes into the urine whenever excessive amounts of it have been ingested. Even a few pieces of candy may suffice at times to produce this effect when the system has already been well stocked with sugar. Obviously, this condition which is known as *physiological* or *alimentary glycosuria*, is only temporary in its nature, while diabetes is characterized by a permanent discharge of excessive amounts of sugar.

The Life History of the Proteins.—The most striking difference between the plants and animals consists in the inability of the latter to manufacture protein material from non-protein substances. Contrariwise, the plants are able to obtain certain salts from the soil and to abstract carbon, hydrogen and some oxygen from its preformed carbohydrates, finally uniting them in certain proportions into the complex molecule of a protein. The nitrogen, sulphur and phosphorus are derived from the salts.

Such foods as the white of eggs, meat, curdled milk, beans, peas, etc. contain their own peculiar types of proteins. All of them are reduced by the different digestive fluids into amino-acids which, however, show certain differences in

accordance with their origin. About twenty amino-acids are known at the present time. These simple building-stones are reunited in the system into the proteins of the body which are later employed by the tissues in the construction of their cellular materials. The proteins, so to speak, form the core of all living animal matter.

We have noted that the proteins are not acted upon in the mouth, but are changed in the stomach by the pepsin and rennin into peptones. A further cleavage takes place in the small intestine in consequence of the action of trypsin and erepsin, but the different amino-acids resulting during this last stage of digestion, by no means possess the same nutritive value. Probably the most useful are the ones derived from meat, although those of milk, potatoes, and rice are also very valuable. These facts should be carefully borne in mind when selecting a suitable diet for those persons whose weight has been greatly reduced by illness. Under these circumstances the carbohydrates are attacked first and then the fats, because these foodstuffs really protect the protein core of the body. Thus, the former will have been fully utilized before the proteins are actually affected. Consequently, in rebuilding the constituents of the body we must first endeavor to furnish an adequate supply of proteins from which the principal mass of the cells can be reconstructed. Beef broth is the most potent nutrient that may be offered to the body at this time. Later on, after the protein content of the cells has been replaced, the body replenishes its store in fat and sugar.

Under ordinary circumstances, however, the best results are obtained when the body is supplied with proteins of different origin. Thus, while it is true that meat is a very concentrated protein food and brings quick results, it may be quite unable to furnish certain "building stones" which are absolutely essential to the cells. It is entirely probable that the latter may require at times the amino-acids derived from vegetables. Obviously, however, vegetables must be eaten in very large amounts in order to satisfy the protein needs of the body, and, again, an exclusively vegetarian diet would be prone to lead to a want of meat proteins.

It should also be noted that certain proteins are quite unable to meet the protein requirements of the body. Such a food is the connective tissue of uncooked meat. It contains collagen which is converted by heat in the presence of water into soluble gelatine. To this class of *albuminoids* also belongs the protein of Indian corn. The amino-acids derived from cellular metabolism, are finally converted into carbon dioxid, water, and several relatively simple substances containing nitrogen. Chief among the latter is *urea*. The most considerable portion of this excretory material is formed in the liver, although it cannot be denied that it may also be manufactured by the tissues at large. Urea circulates in a soluble form, and is finally removed from the blood by the cells of the kidneys. Hence, these organs do not actually manufacture it, but simply transfer it to the urine.

The Life History of Fat.—Like the carbohydrates, the fats consist of carbon, hydrogen and oxygen, but oxygen is present in relatively small amounts. They do not contain nitrogen and are insoluble in water. Probably the most familiar compounds of this kind are the fat of meat, butter, olive oil, and lard. The saliva is powerless to act upon these substances, and so is in a large measure the gastric juice. In the small intestine, however, they are decomposed into fatty acids and glycerin. Soaps are formed here in the presence of alkalies. While traversing the lining cells of the intestine, these simple elements are rebuilt into neutral fat of a variety peculiar to the animal. They are then transferred into the lymphatics of the villi, *i.e.*, into the lacteals. It has been stated above that the contents of these absorbing channels assume a milky appearance when loaded with the rebuilt globules of fat.

In general, it holds true that the different foodstuffs serve a twofold purpose after their absorption into the body. Thus, they may be burned up directly by the cells to yield energy or may first be stored as an intricate part of their cytoplasm. Concerning the fats it should be mentioned that they are finally reduced into their characteristic end-products carbon dioxid and water. As has already been alluded to, a portion of them always serves the immediate oxidative

needs of the body, while another portion is either stored as such or is modified to enter into the combination of the substance of the cells. The former may be termed *circulating fat* and the latter, *tissue fat.* A similar terminology may be employed in the cases of the proteins and carbohydrates to designate their fate.

When fully oxidized fat yields carbon dioxid and water. It serves as a very important source of energy. This being the case, the body always retains a considerable portion of it in the form of *stored fat.* This depôt-fat is mobilized and transported to the tissues whenever the latter have used up their own store of energy-yielding material. Fat is stored in the so-called *adipose tissues;* for example, in the subcutaneous connective tissue, where it appears as globules within the intracellular material. This depository is usually designated as the *panniculus adiposus.* Other store houses are the shafts of the long bones, the region around the kidney, the mesentery, and the liver. The average human adult gives lodgment to about 10 kg. of fat.

CHAPTER XXVII

THE METABOLIC REQUIREMENTS OF THE BODY ANIMAL HEAT

Calorimetry.—Under ordinary circumstances, about nine-tenths of the food ingested passes into the absorbing channels, and eventually leaves the body in the form of various excretory products. It is true, however, that the quantity of the food taken in is usually much larger than is actually required to cover the metabolic needs of the body. This ingestion of food in excess of that necessary to balance the waste, is called *luxus consumption*. Obviously, an intake in decided excess of actual requirements must lead to a greater escape of still useful substances into the large intestine.

The food which has been absorbed, possesses a composition rendering it well adapted for the oxidations taking place in the cells of the tissues. In principle, these processes do not differ from those constantly occurring in atmospheric air, because sugar and fat may also be oxidized outside the body under liberation of carbon dioxid and water. It is true, however, that the cells are able to make a greater economical use of these materials than could be obtained by their combustion outside the body.

We are well aware of the fact that oxidations and combustions yield heat, and that the value of any combustible material, such as wood or coal, may be ascertained directly by measuring the heat derived from it when burned in the presence of oxygen. Very similar tests may be made with the different foodstuffs. A measured quantity of them is placed in a special metal receptacle and reduced in the presence of oxygen. The term of *bomb-calorimeter* is applied to these simple heat indicators. Besides, it is possible to ascertain the heat given off by an animal during a certain

period of time by placing it in an apparatus which is known as a *calorimeter*. The animal may then be fed with the different foodstuffs to determine their value in terms of heat liberated by it. In its most complete form an instrument of this kind consists of an air-tight chamber which is sur-

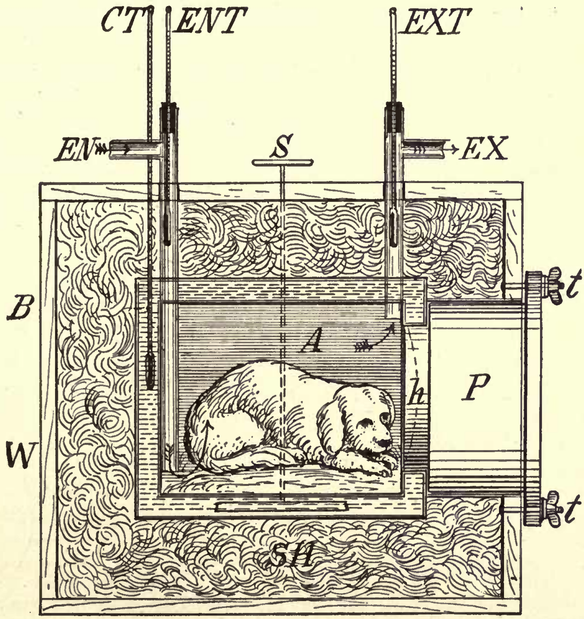


FIG. 106.—Water calorimeter. *A*, inner compartment for animal; *SH*, space filled with non-conductile material; *ENT* and *EXT*, tubes for the respiratory air; *CT*, thermometer in jacket filled with water; *S*, stirrer to equalize the temperature of the water. (*Reichert.*)

rounded by a jacket filled with water. The temperature of the water is measured by means of a thermometer. In order to protect this entire apparatus against undue loss of heat, it is invested with a layer of felt, a material conducting heat very poorly. The inside compartment is connected by means of a tube with a respiration apparatus, furnishing a definite quantity of air in a given period of time. Further-

more, the ingoing and outgoing air may be analyzed in order to be able to determine the amount of carbon dioxid given off by the animal during its stay in the calorimeter. In addition, the character and composition of the ingesta and excreta are carefully noted so as to be able to ascertain the energy supply and waste. In recent years the size of these compartments has been increased sufficiently to accommo-

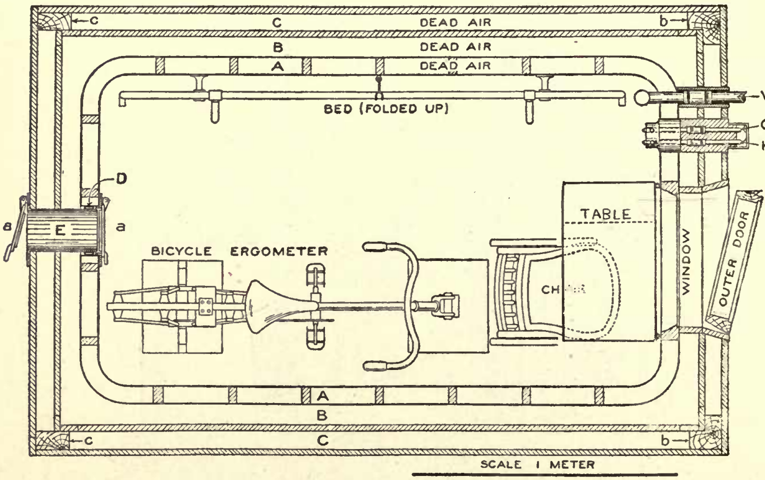


Fig. 107.—Schematic outline of the respiration calorimeter. *A*, dead air space between copper and zinc walls; *B*, dead air space between zinc wall and wooden wall; *C*, dead air space between inner and outer wooden walls. *E*, tube for food; *S* and *H*, inlet and outlet for water; *A*, air circulation. (*Atwater and Benedict.*)

date persons whose metabolic requirements are to be tested. These large *respiration-calorimeters* possess the general character of a small room, in which the person selected for the experiment may move about and be subjected to various tests related to the subject of inquiry Thus, he may be made to ride a stationary bicycle in order to determine the metabolic changes evoked by perfectly definite amounts of work.

The Calorie.—We have previously noted that the amount of mechanical energy liberated by a person may be expressed

in terms of work. Thus, we speak of the work performed by lifting a weight of one kilogram to a height of one meter as a kilogrammeter. In seeking an equally exact unit of measurement for the energy liberated in the form of heat, use is commonly made of the *large calorie*, *i.e.*, the amount of heat required to raise the temperature of one kilogram of water by one degree centigrade. We also speak at times of the *small calorie*, which refers to the amount of heat needed to raise the temperature of one gram of water by one degree of centigrade. Supposing, therefore, that the quantity of water in the calorimeter weighs 10 kg. and that its temperature rises 1° C. every half-hour, the amount of heat liberated by the animal during this time, amounts to 10 calories, or to 480 calories in the course of twenty-four hours.

The Energy in Food.—Inasmuch as the body is never in a condition of complete rest, it cannot justly be compared to a machine. We know that the latter does not consume energy when its movements are arrested. The body simply shows phases of comparative rest alternating with periods of activity, during which the heart, respiratory organs, and glands continue to fulfill at least a part of their usual duties. Consequently, the evolution of heat can only be determined with accuracy when the aforesaid tests are continued for long periods of time.

It should also be remembered that the balancing of the ingo and outgo is a relatively simple matter in the cases of the carbohydrates and fats, because these foodstuffs are completely oxidized in the organism into carbon dioxid and water. The proteins, on the other hand, are not fully reduced, because their nitrogenous end-product, urea, still contains a recognizable amount of energy. Their full value as a fuel, therefore, can only be ascertained if the amount of energy contained in the urea is added to the physiologically available heat derived from them. It has been determined that 1 gram of sugar yields 4 calories, and 1 gram of starch a trifle in excess of this figure. Fat, on the other hand, furnishes 9.3 calories for each gram of substance and protein 4.8 calories. As has just been stated, a certain amount of

the energy contained in the latter is lost with the urea, because 1 gram of protein burned in the open yields more than 6 calories. Thus, it may be stated that the aforesaid food stuffs give the following results:

1 gram of protein	4.1 calories
1 gram of carbohydrates	4.1 calories
1 gram of fat	9.3 calories

The Energy Requirement of the Body.—Heat is lost not only by radiation but also in the form of bound heat. Hence, a person living in a calorimeter furnishes not only a certain portion of heat to warm up the water in the apparatus, but also a certain amount which is really "latent," because it is lost through the evaporation of the sweat. It is conceded that a person may evaporate about one liter (1000 grams) of water in the course of twenty-four hours. This change from the liquid to the gaseous state requires heat amounting to about 500 calories. Obviously, this correction must be made when the total heat liberated by the person is to be computed.

By taking all these factors into consideration, it has been found that a person, when sleeping, requires one calorie per hour for each kilogram of weight. Hence, a person weighing 70 kg., needs about 1700 calories to balance his material metabolic requirements. The consumption of energy which just covers the needs of a resting person, is known as *basal consumption* or *basal metabolism*.

The heat production and energy requirement of a person increases considerably when work is done. Muscular activity is the chief factor to be considered in this connection, because even during comparative rest the basal metabolism rises to 2100 calories, and reaches the value of 2500 calories when light work is done. Moderate work requires 3500 calories and heavy work 4000 to 10,000 calories.

The Caloric Value of Foods.—In order to obtain the required number of calories, use is made of such foods as are included in the accompanying table. It will be seen that they differ greatly in their chemical composition and possess, therefore, different caloric values.

	Water	Protein	Starch	Sugar	Fat	Salts
Bread	37	8	47	3.0	1.0	2.0
Wheat flour	15	11	66	4.2	2.0	1.7
Oatmeal	15	12	58	5.4	5.6	3.0
Rice	13	6	79	0.4	0.7	0.5
Peas	15	23	55	2.0	2.0	2.0
Potatoes	75	2	18	3.0	0.2	0.7
Milk	86	4	..	...	24.0	0.8
Cheese	37	33	..	...	3.0	5.0
Lean beef	72	19	..	...	29.0	1.0
Fat beef	51	14	..	...	.....	1.0
Mutton	72	18	..	...	5.0	1.0
Veal	63	16	..	...	16.0	1.0
White fish	78	18	..	...	3.0	1.0
Salmon	77	16	..	...	5.5	1.5
Egg	74	14	..	...	105.0	1.5
Butter	15	..	..	...	83.0	3.0

As a rule our diet is arranged to yield about 3000 calories. The relative proportions of the three principal foodstuffs are: 75 grams of proteins, 90 grams of fats, and 550 grams of carbohydrates. These substances furnish the following number of calories:

Protein	70 grams	=	280 calories
Fat	90 grams	=	810 calories
Carbohydrates	550 grams	=	2200 calories
			3290 calories

It is easily apparent that the carbohydrates and fats bear the brunt of the metabolic requirement, while protein retains a relatively constant substratum value. Hence, any additional demand would have to be met chiefly by a greater intake of the former foodstuffs. This is easily explained, because a healthy adult person, taking a fair amount of exercise, eliminates about 300 grams of carbon and 20 grams of nitrogen, or about $1/15$ as much nitrogen as carbon. In order to derive this quantity of carbon from meat, about 1800 grams or 4 pounds of lean beef would have to be eaten, while more than the required amount of nitrogen can be obtained from 453 grams or 1 pound of it. Consequently, a person who derives his fuel chiefly from protein, overtaxes his digestive and excretory organs, and follows, moreover, an unsound economic path.

For this reason, a mixed diet is the only one which can be justified physiologically. It is true, however, that most foods constitute a mixed diet in themselves. Thus, meat contains not only protein substances, but also from 30 to 50 per cent. of fat, while bread embraces the protein, glutin, as well as starch, sugar, and minute quantities of fat. Likewise, milk furnishes water, salts, casein, albumin, emulsified fat, and milk-sugar or lactose. Milk, however, contains no iron, which is required by the body in forming the hemoglobin of the red blood corpuscles.

Conditions of life may be such, however, that a well balanced mixed diet cannot be maintained for long periods of time. Thus, we find that the Esquimaux are forced to live chiefly upon proteins and fats and must derive their body-sugar from the excess protein. It has been mentioned above that the surplus protein may become a source of sugar and fat. The other extreme is presented by the vegetarians who reduce their ingestion of proteins to a minimum, although the addition of milk and eggs to their diet would raise it practically to the standard of a mixed diet. Nuts and vegetable oils furnish their requirement in fat.

The Body-temperature.—Every cell in our body is a producer of heat. Admittedly, however, tissues differ greatly in their activities and hence, also in their power of liberating heat. No doubt, the most important heat-generating organ is the skeletal muscle tissue, because we well know that even a very moderate form of muscular exercise quickly raises our body-temperature two or three degrees.

The heat liberated by the cells of the different tissues, is transferred in largest part to the blood which again transfers it to the air. Thus, it has been found that the average temperature of the blood traversing internal channels is 39° to 40° C., while that of the blood in the more exposed vessels is only 28° to 35° C. It will be seen, therefore, that the production of heat is balanced by a definite loss, and that the product of the interaction between these two factors represents the temperature of the body. It is common knowledge that the body-temperature retains a relatively constant value in some animals and an inconstant value in

others. The former are commonly designated as *warm-blooded* and the latter, as *cold-blooded* animals.

This difference suggests that the warm-blooded animals are in possession of a mechanism by means of which the heat of their body is stagnated in amounts just sufficient to give them a practically uniform temperature. Contrariwise, the cold-blooded animals must lose their heat almost as rapidly as it is formed, because they have no means of regulating its escape. This statement leads us to infer that their body-temperature must be equal to that of the surrounding medium, although it can never quite reach the latter value, because the metabolism of even the most quiescent animal cannot be made to cease altogether. For this reason, a frog living in water of 20° C., shows a body-temperature of about 21° C. Warming the water to 30° C. raises its body-temperature to about 31° C., while cooling it would produce the opposite effect.

In this connection, it should also be remembered that the body-temperature of even the warm-blooded animals may be varied by outside influences, but usually only within tenths of one degree. Thus, our body-temperature reaches its lowest point early in the morning and its highest level late in the afternoon. These changes, however, rarely amount to more than 1.2° C., and fluctuate around the normal value of 37° C. or 98.4° F. The body-temperature is usually ascertained by placing a clinical thermometer under the tongue, meanwhile protecting it against radiation by closing the lips. When measured in the rectum, the temperature is somewhat higher, namely, 37.3° C. Children possess a higher body-temperature than adults, because they are more active.

The Regulation of the Body-temperature.—A uniform body-temperature can only be obtained if the production and dissipation of heat are accurately balanced. Thus, a rise in the body-temperature may be due either to a greater heat production or a diminished dissipation, or both. Heat production may easily be reduced by muscular rest, and increased by exercise. The same results follow the varying activity of the glandular structures.

Heat dissipation is regulated in two ways: namely, *volitionally* and *non-volitionally* by reflex action. Thus, the dwellings of man are constructed to resist changes in the temperature of the air, and different clothing is worn to correspond to the time of day and the seasons of the year. Besides, the body is in possession of several mechanisms by means of which the loss of heat may be controlled in a reflex manner. Chiefly concerned in this regulation are those nervous parts which vary the caliber of the bloodvessels and the activity of the glands. It is easily conceivable that the dilatation of the bloodvessels of the skin must favor heat dissipation, because a larger amount of blood is then exposed to the neighboring air. Contrariwise, the constriction of the cutaneous vessels must tend to conserve the heat, because the vessels of the skin are thereby rendered relatively bloodless. In this regard, therefore, the bloodvessels may be likened to the pipes of a heating apparatus. The heat imparted to their contents by innumerable minute furnaces situated in the cells of the tissues, is transferred by them in part to the air.

A very important factor concerned in this process of regulating the body-temperature, is the sweat. If the skin is thoroughly moistened with this secretion, a much greater amount of heat will be lost than when it is relatively dry. Ordinarily, the dilatation of the cutaneous vessels is associated with a more copious production of sweat, both changes becoming more intense when a greater heat—dissipation is to be effected. Contrariwise, the constriction of the bloodvessels of the integument usually diminishes the quantity of this secretion, because this general reaction reduces in most instances also the bloodsupply of the sweat glands. A similar function is performed by the water moistening the lining of the respiratory passage. Thus, those animals whose integument is covered with a thick coat of hairs, a poor conductor of heat, rid themselves of their superfluous heat by the act of panting. The respiratory air is then forced in quickly repeated draughts across the moistened mucous membranes of the mouth and upper air-passage so as to increase evaporation.

A similar means of heat dissipation is resorted to by us during muscular exercise. It consists in increasing the frequency and depth of the respiratory movements. While the primary purpose of this greater ventilation of the lungs is the augmentation of the gas exchange, it also facilitates the discharge of heat through this channel by radiation as well as by the evaporation of the moisture. When exercising, the body is constantly brought in contact with fresh layers of air which have not been warmed up as yet. Thus, slight movements afford the same relief as an electric fan, because they bring the surface of our skin in relation with cooler air.

The foregoing discussion leads us to infer that the heat of the body is dissipated directly by radiation and conduction, as well as indirectly by evaporation. By *radiation* is meant the transfer of the heat to another body through space without causing an appreciable change in the temperature of the air. But, heat may also be *conducted* from one body to another by contact. Thus, if the hand is placed against a cold window pane, it gives off heat to the glass, while the latter in turn loses it to the adjoining layers of air. Quite similarly, a person immersed in cold water, transfers his surplus heat to the medium which in turn warms up the walls of the receptacle and adjoining air. Heat is also lost through the medium of the water discharged by the body, because the evaporation of every globule of it necessitates the expenditure of a certain portion of this energy.

Attention has already been called to the fact that humid and warm air produces a certain discomfort, because it prevents the dissipation of heat by lessening evaporation. The sweat then accumulates upon the surface of the body in visible drops, each of them retaining a certain amount of bound heat. A dry atmosphere, on the other hand, favors evaporation. The skin then becomes relatively dry, although the amount of water actually lost by it may be greater than in the former instance. Thus, the stoker in the engine room is able to toil in a hot atmosphere, because he secretes a very copious quantity of sweat which is quickly taken up by the heated air. A person working in a passage under ground, might really be in a less favorable situation than the

stoker, because while the air is cooler here, its greater relative humidity retards the loss of bound heat.

Fever.—Temporary rises of the body-temperature above normal are produced most easily by muscular exercise. In this case, the heat-production is augmented so rapidly that it cannot be compensated for completely until several minutes thereafter. Rises of a more permanent kind may be evoked by working in a humid and warm atmosphere, because in this instance the greater production of heat is antagonized by a lessened dissipation. It is a well known fact that the entrance into the body of certain disease producing bacteria gives rise to a rather prolonged elevation of the body-temperature which is commonly designated as *fever*. As in the above instances, this condition must be brought about by a disproportionate relationship between heat-production and heat-dissipation, leaving a positive balance for the body-temperature.

The chief factor, however, seems to be a disturbance of the dissipating mechanism which produces a stagnation of heat even at a time when its production remains practically the same. A sensation of *chilliness* is usually experienced at the beginning of a fever, because the superficial bloodvessels then constrict, causing in turn a cessation of the secretion of sweat. As the skin cools, certain reflexes are evoked, the purpose of which is to counteract the fall in the body-temperature. Even the smooth muscles of the skin contract in an endeavor to prevent this loss by pressing upon the cutaneous vessels. The regions of the roots of the hairs and pores are thereby made to project from the surface in the form of minute papillæ, giving rise to an appearance of the skin which is generally known as *goose-flesh*. The muscles are made to quiver in an endeaver to produce a surplus amount of heat in order to overcome the sensation of chilliness. The temperature now rises very rapidly, while the patient appeals for heavier covers. The skin becomes flushed and feels distinctly hot.

Later on in the course of the fever, the production of heat is materially diminished, but since the constriction of the cutaneous vessels continues, its dissipation must still be too

slight to cause a decided lowering of the body-temperature. The "breaking-point" of the fever is indicated by a gradual return of the body-temperature to normal. The skin then loses its livid, flushed appearance and is again moistened with sweat. Large amounts of urine are secreted, its color gradually becoming lighter. The activity of the heart and respiratory parts decreases constantly until normal conditions have again been established.

Fever is not altogether a pathological process, but constitutes really a physiological reaction of the cells to bacteria and their products. In fact, it may also be a protective means, because many bacteria are killed at a temperature of 38° to 40° C. It is true, however, that the increased production of heat is associated with a disturbance in the dissipation of the body-heat, which is brought about chiefly by the constriction of the cutaneous vessels and the cessation of the secretion of sweat. During this period of increased metabolism, the cells oxidize principally the stored proteins and not the fats and carbohydrates.

CHAPTER XXVIII

EXCRETION

The Excretory Channels.—The term excretion is commonly applied to that process which purposes to remove the waste matter from the body. In its passage through the different tissues, the blood is incessantly loaded with the products of cellular decomposition. It follows that if this medium is to be kept in a proper functional condition, these waste substances must be removed from it almost as quickly as they are formed. The organs which are directly concerned with this elimination, are the lungs, kidneys, skin, and alimentary canal. The chief gaseous excretion is furnished by the lungs in the form of carbon dioxid. It constitutes the final product of the metabolism of the carbon of the food. Water is discharged by the kidneys, skin, intestinal canal, and the mucous lining of the pulmonary passage. The excretion of the kidneys also embraces the various end-products of protein metabolism, such as urea, creatin and creatinin.

The waste from the intestine is of miscellaneous character, and finds its origin in the excrements of the bile. The loss of water by this route is inconsiderable under normal conditions. The discharge of carbon dioxid has already been discussed in detail in a preceding chapter, so that we are now able to direct our attention more particularly to the excretory functions of the kidneys and skin.

The Kidneys.—The kidneys are situated in the lumbar regions of the abdominal cavity, one on each side of the spinal column. Each organ measures about 100 mm. in length, 50 mm. in breadth, and 25 mm. in thickness. It occupies the space between the upper borders of the 12th thoracic and third lumbar vertebræ. Its shape is similar to that of a bean, its concave side being directed toward the spinal column. Near the center of this concavity is a decided depres

sion, known as the hilum, through which the bloodvessels and nerves enter this organ. The channel supplying it with nutritive material is called the *renal artery.* It arises directly from the abdominal aorta. The venous drainage of this organ is conveyed by the *renal vein* into the inferior vena cava. In addition, the hilum also serves as the point of

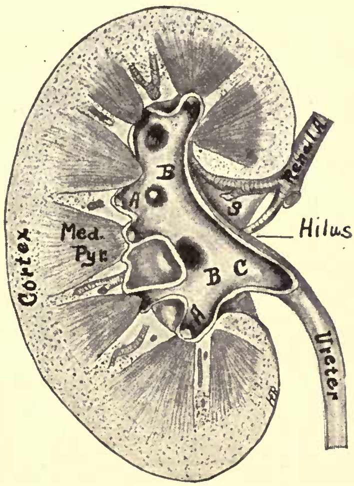


FIG. 108.—Median longitudinal section through the right kidney. *A*, *A*, calyces minores; *B*, *B*, calyces majores; *C*, pelvis of the ureter; *S*, hilus of the kidney. (*Radasch.*)

exit for the *ureter,* a musculo-membranous tube by means of which the secretion of the kidney is conveyed into the urinary bladder.

Each kidney rests upon a cushion of adipose tissue, and is invested by a dense *capsule* of connective tissue. When cut across longitudinally, it presents three distinct zones: namely, an outer one or *cortex,* a middle one or *medulla,* and an inner one or *pelvis.* This structural peculiarity is dependent upon the manner in which the functional element of this organ is arranged. It is to be noted first that each kidney is composed of a very large number of tubular glands, which begin in its cortical substance and terminate at the junction

between its medullary portion and the pelvis. This inner membranous receptacle of this organ really represents the enlarged upper extremity of the ureter.

The Uriniferous Tubule.—The tubular glands of which each kidney is composed, are called *uriniferous tubules*. They are concerned with the secretion of the urine. Each tubule furnishes a small globule of this excretion which is conveyed into the pelvis, where it is added to those secreted

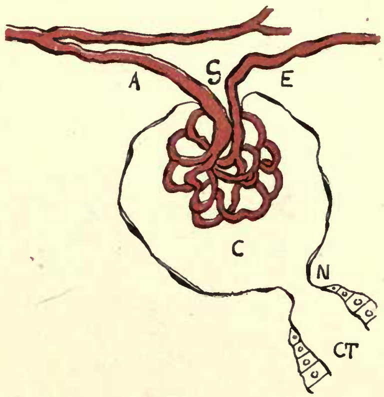


FIG. 109.—Glomerulus with the beginning segment of the uriniferous tubule. *G*, glomerulus; *A* and *E*, afferent and efferent blood-vessels; *C*, capsule of Bowman; *N*, neck of uriniferous tubule; *CT*, distal convoluted tubule.

by the other tubules. It is easily understood that the constant influx of urine from the different glands must finally lead to a distention of the walls of this reservoir and evoke certain reflexes which cause its muscle fibers to contract. The purpose of this contraction is to force the contents of the pelvic reservoir into the ureter proper, whence they are propelled into the bladder. The movements of the ureter bear a close resemblance to those previously observed in the œsophagus, stomach, and intestines. They are peristaltic in character, and invariably pursue a course from above downward. These waves recur at brief intervals, every one of them forcing a droplet of urine into the bladder.

Each urinary tubule begins in the cortex (bark) of the kidney in a rounded dilatation which is known as the *capsule*

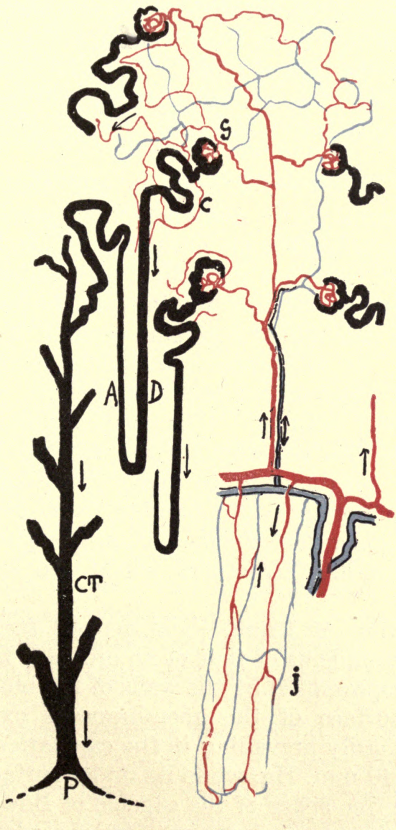


FIG. 110.—Diagrammatic representation of the blood-supply and course of the uriniferous tubule. *J*, interlobular blood-vessels derived from arches between cortex and medulla; *G*, glomeruli; *C*, distal convoluted tubule; *D* and *A*, descending and ascending limbs of the loop of Henle; *CT*, collecting tubule; *P*, papilla and pelvis of the kidney.

of Bowman. A coil of capillaries is freely suspended within this capsule in such a way that it forms contact with the

wall of this cavity only at the point where the arterial supply channel enters. The term *glomerulus* or *Malpighian corpuscle* is usually applied to this entire structure. After leaving the capsule, each tubule pursues a serpentine course and is then reflected upon itself to form a U-shaped segment which is called the *loop of Henle.* Distally to this point, the tubule again describes several irregular curves, and finally unites with others into a *collecting channel* which opens into the pelvis.

In general, therefore, it may be said that each tubule embraces a *central* and a *distal convoluted portion,* these segments being separated from one another by the loop of Henle. Because of the fact that the collecting tubules and loops of Henle strive in a radial direction towards the pelvis, while the glomeruli and convoluted segments occupy the outer region of this organ, its substance seems to be composed of two distinct layers which, as has been stated above, are designated as its cortex and medulla. This peculiar distribution of the urinary tubule also accounts for the striated appearance of its medullary portion. Since many collecting tubules are always bound together into bundles, each group of which possesses a single orifice, the medulla appears in the form of a number of fan-like structures which are known as the *pyramids.*

The Secretion of Urine.—The general structure of the glomerulus reminds us of that of an ordinary filter, in which the paper is represented by the walls of the blood-capillaries. The upper surface of this membrane is exposed to the pressure ordinarily prevailing in the capillaries and amounting to about 40 mm. Hg, while its under surface lies in relation with the free space of the capsule of Bowman in which the pressure is practically zero. In accordance with this structural peculiarity it was assumed at an early date that the secretion of urine is entirely dependent upon the physical factor of differences in pressure. This assumption justified the early view that the capillary lining permits every constituent of the blood to pass through, excepting, of course, the formed elements. In accordance with this conception, the glomerulus was supposed to yield urine in its complete form.

Repeated experimentation, however, has proved that the secretion of urine is by no means a process of simple filtration, because the capillary lining of the glomerulus lets certain constituents of the blood pass through freely, while it prevents the escape of other very similar substances. In order to be able to explain this discrepancy, the factors of diffusion and osmosis were added to that of filtration. In further analysis of this subject-matter it was then observed that while the three factors just enumerated play a very important part in the formation of urine, the cells of the urinary tubule no doubt exert a decided influence upon the character of this secretion. In other words, there has been added to the three aforesaid factors a fourth one, embracing the minute chemico-physical properties or vital activity of the cells lining the urinary tubule. Thus, it has finally been concluded that the water and inorganic salts of the urine are formed in the glomeruli, while the cells of the adjacent convoluted tubules add to this secretion its organic constituents. Hence, it may be said that the urine becomes more concentrated as it traverses the convoluted tubule.

The Composition of Urine.—The renal secretion is a clear fluid, possessing a light straw-color and a specific gravity of about 1.020. Its reaction, which is moderately acid, is due to the presence of acid sodium phosphate. On standing the urine becomes alkaline, because its chief constituent urea is then decomposed under production of ammonium carbonate. It then emits an ammoniacal odor and becomes cloudy.

A healthy person secretes about 1500 c.c. (50 ounces or 2½ pints) of urine in the course of twenty-four hours. Its quantity, however, may be varied considerably in different ways: for example, by increasing or decreasing the intake of water and by altering the activity of the sweat glands. Inasmuch as a direct relationship exists between these excretory organs, it is evident that a more copious secretion of sweat must diminish the amount of urine. The latter then becomes much darker in color and more concentrated.

The urine contains: (*a*) inorganic material in the form of sodium chlorid and the sulphates and phosphates of sodium,

potassium, calcium and magnesium; (*b*) organic material, chiefly in the form of urea; (*c*) coloring material which is derived from the reduced pigments of the bile; and (*d*) traces of certain gases, such as carbon dioxid, nitrogen, and oxygen. The sodium chlorid possesses no metabolic history, and simply leaves the body through this channel in amounts proportionate to those ingested. The sulphates and phosphates, on the other hand, are derivatives of the proteins which leave the body in these particular combinations.

Urea is not made in the kidneys, but is merely picked out by these organs from the blood and transferred into the lumen of the urinary tubule. It is formed in the liver from the protein waste of different tissues, principally that of the muscles, and also from the superfluous nitrogen of the food. A normal adult eliminates about 30 grams of this substance in the course of a day, but this quantity may be greatly increased by muscular exercise as well as by a surplus ingestion of proteins. Inasmuch as the protein content of the body remains relatively stationary, nothing can be gained by consuming excessive amounts of this foodstuff. In fact, the only result would be an overtaxing of renal function which would become the more dangerous when only small amounts of water are taken. It has been stated elsewhere that urea represents the nitrogenous product of the cleavage of the protein molecule, although a portion of it, namely, one-eighth of the total, is transformed into other more complex constituents, such as uric acid and creatin.

The urine also contains traces of sugar and albumin. Whenever these constituents appear in appreciable amounts, they are indicative of a disturbance in renal function. A temporary glycosuria, as we have seen, may be perfectly physiological, because it merely serves to eliminate surplus amounts of sugar. Likewise, a temporary albuminuria may follow severe muscular exercise. The urine also contains traces of indican, a constituent derived from the putrefaction of the protein food in the large intestine. Excessive amounts of this substance would suggest a corresponding increase in the putrefaction of this foodstuff. A similar

body is acetone. Its origin is to be sought in an incomplete oxidation of the fats and possibly also of the proteins.

The Storage of Urine.—The purpose of the successive peristaltic waves descending along the ureter, is to transfer the contents of the pelvis at intervals into the urinary bladder. The latter presents itself as an oval musculo-membranous pouch which is lined internally by mucous membrane and externally by peritoneum. It is situated in the pelvis behind the pubic bone, its size and shape varying somewhat with the amount of urine contained therein. The *ureters* pierce its posterior and inferior wall at some distance from one another and in a slanting direction. This arrangement serves the purpose of a sphincter, because the gradual distention of the bladder gives rise to a compression of these orifices. The lower pole of the bladder gradually tapers into a narrow membranous canal, the *urethra,* which opens to the outside by an orifice, known as the *urinary meatus.* The point of union between this canal and the tapering end or neck of the bladder is marked by two conspicuous bands of circular muscle tissue which are termed the *internal* and *external sphincters* of the urethra. These fibers are normally held in a condition of tonus, so that the urethra is kept free from urine during the interims between the acts of micturition.

When empty, the urinary bladder presents a shriveled up appearance. For this reason, the inflow of urine through the ureters cannot at first establish a considerable pressure within its cavity. Later on, however, when its walls have become somewhat distended, the pressure rises more rapidly, reaching its maximal value of about 150 mm. H_2O at a time when about 250 c.c. of urine have been collected therein.

The voiding of the urine constitutes the act of *micturition.* The factors involved in it are the contraction of the walls of the bladder and the relaxation of the sphincters of the urethra. An additional rise in pressure may be produced by the contraction of the abdominal musculature. The local motor mechanism of the bladder is under the control of a simple reflex center which is situated in the lumbar segment of the spinal cord. Its activation is accomplished by the different impulses generated in consequence of the distention of

the walls of the bladder. It should be remembered, however, that in the adult mammal the opening of the sphincters and contraction of the musculature of this organ may be inhibited for a time by the higher cerebral centers.

The Skin as an Excretory Organ.—The skin consists of an outer layer or *epidermis* and an inner layer or *dermis*. Below the latter lies a loose reticulum of fibrous connective tissue which is often greatly infiltrated with fat and forms the so-called panniculus adiposus. The epidermis is composed of many layers of flat cells, the outermost of which are constantly lost and replaced by those occupying the next stratum. Those of the deepest layer possess a certain thickness and multiply by cell-division, whereupon they move outward toward the surface of the body. Since the epidermis is devoid of bloodvessels, these cells undergo retrogressive changes and are finally converted into flat, scale-like platelets.

FIG. 111.—Diagrammatic representation of the skin, showing the location of the sweat glands. *H*, horny layer; *L*, stratum lucidum; *M*, Malpighian layer; *P*, corpuscles of Paccini; *PL*, papillæ of the cutis vera; *C*, cutis vera; *S*, sweat gland; *SC*, subcutaneous tissue.

The deep skin or dermis also consists of two zones: namely, a superficial or papillary layer and an inner or reticular layer. The dermis is made up of a dense network of connective tissue fibers in which are imbedded many elastic fibers. It also embraces many sensory corpuscles and glands. The former are modified end-organs of nerves, and subserve the sensations of touch, pain, and temperature. The glands of the skin appear in two forms: namely, as sweat glands and as sebaceous glands. Their

number varies considerably in different areas of the body. Thus, the sweat-glands are very numerous upon the palms of the hands and the soles of the feet. As many as two or three thousand may be found here in a square inch of skin.

Each sweat-gland consists of a coiled-up portion and a duct. The latter possesses a length of about 0.8 cm. (one-fourth of an inch), and pursues a serpentine course through the outer layers of the skin, opening finally by means of a pore upon its surface. The coil is surrounded by a dense network of capillaries. The secretion furnished by these glands is very watery, containing a small amount of salts, fatty acids, carbon dioxid, and traces of urea. Its content in urea, however, may be markedly increased when the kidneys are not in a proper functional condition. For this reason, persons are made to produce copious amounts of sweat whenever they show an intoxication in consequence of the accumulation of the products of protein metabolism. Attention has already been called to the close relationship existing between the quantity of the urine and that of the sweat. Obviously, if considerable amounts of water are lost through the sweat-glands, the kidneys cannot eliminate their normal quantity of urine. The functions of both organs may in turn be influenced by the escape of water into the large intestine. Thus, watery stools invariably diminish the secretion of urine as well as that of sweat.

Under normal circumstances, the sweat is evaporated from the surface of the skin almost as quickly as it is formed. It is then called *insensible perspiration*. But when the body is exposed to a warm and humid atmosphere, or when a greater amount of sweat is produced than can readily be evaporated, it accumulates upon the surface in the form of drops. We then speak of it as *sensible perspiration*. Under average conditions, close to one liter of sweat is excreted in the course of twenty-four hours. This quantity may be greatly increased by exercise.

The *sebaceous glands* are small globular glands which usually lie in relation with the roots of the hairs, but may also occur independently of these appendages. They furnish an oily secretion, containing fats, epithelial cells, inorganic

salts, and albuminous matter. Its principal purpose is to form a protective layer on the surface of the skin, thereby keeping the integument and the hairs in a soft and pliable condition. The glands situated in the skin of the nose and forehead, are usually very large, and their excretory ducts are frequently plugged with sebaceous material that furnishes a fertile soil for the growth of the ordinary pus-microbes. It is also of interest to note that the sebaceous glands of the external auditory canal furnish a modified secretion which contains a yellowish pigment and hardens on exposure to the air. This waxy material is called *cerumen*. On occasions it may form a solid mass of material which completely blocks the entrance to the middle ear, thereby greatly impairing the vibration of the ear drum and diminishing the acuity of hearing.

The skin also contains numerous smooth muscle cells which usually lie in relation with the roots of the hairs. Their contraction is effected reflexly in consequence of emotions and the stimulation of the integument by cold. Inasmuch as these cells are directed almost transversely to the roots of the hairs, their contraction must cause the shafts of these appendages to assume a more vertical position. This mechanism is brought into play by many animals as a means of protection against their natural enemies. Probably the most familiar reactions of this kind are the erection of the hairs upon the tail and dorsal aspect of the cat's body, and the erection of the bristle-like appendages and spines of the porcupine.

CHAPTER XXIX

THE INTERNAL SECRETIONS

Classification of the Endocrine Organs.—The subject-matter of the internal secretions is a comparatively recent one. It is concerned with the functions of those glandular bodies which do not possess a recognizable excretory duct, and pour their products directly into the blood or lymph. Usually insignificant in size and tucked away in out of the way places of the body, these endocrine structures failed to attract attention until about the year 1880, when it was proved that the total removal of the thyroids for the relief of the disturbing symptoms associated with goiter produced death within a relatively short period of time. Contrariwise, it was noted that the partial removal of this gland did not give rise to any untoward effects. More recently, these observations have been repeated upon the adrenal bodies, pancreas, and other organs of this character. Inasmuch as the removal of any one of these structures by operative means, accidental injuries, or pathological processes invariably results in dangerous consequences to man and the mammals in general, it can no longer be doubted that these glands exert a powerful influence upon the functions of the body.

The chemical nature of the products of the endocrine organs is not fully known, although it is possible to employ them in an experimental way. For this purpose we usually prepare them by macerating and extracting the gland as a whole in a solution of 0.7 per cent. sodium chlorid, this extract then being injected directly into the bloodstream to see what effects it produces. In the case of the adrenal bodies, the active principle has been isolated and is now sold in the form of a commercial preparation, known as adrenalin. A somewhat similar "purification" has been attained in the case of the active agent of the extract of thyroid gland.

The organs belonging to the group of the endocrines (Greek: within, to separate), are the thyroids, parathyroids, thymus, adrenals or suprarenal capsules, pancreas, liver, pineal gland, pituitary body, testes, and ovaries. Every one of these structures furnishes a product which is essential to the life of the animal. The general term employed to designate these drug-like principles, is autacoid substances (Greek: remedy, natural). But since they may accelerate as well as retard a certain function, they are usually divided into two groups, embracing, on the one hand, the hormones (Greek: to excite) and, on the other, the chalones (Greek: to make slack). A typical hormone is the secretin of the duodenal mucosa which stimulates the flow of the pancreatic juice. Among the chalones might be mentioned the active agent of the adrenals which prevents the excessive mobilization of the glycogen of the liver.

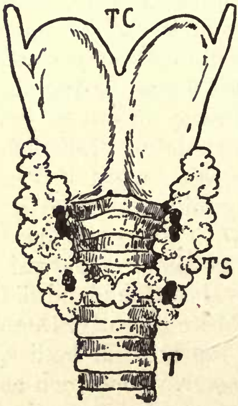
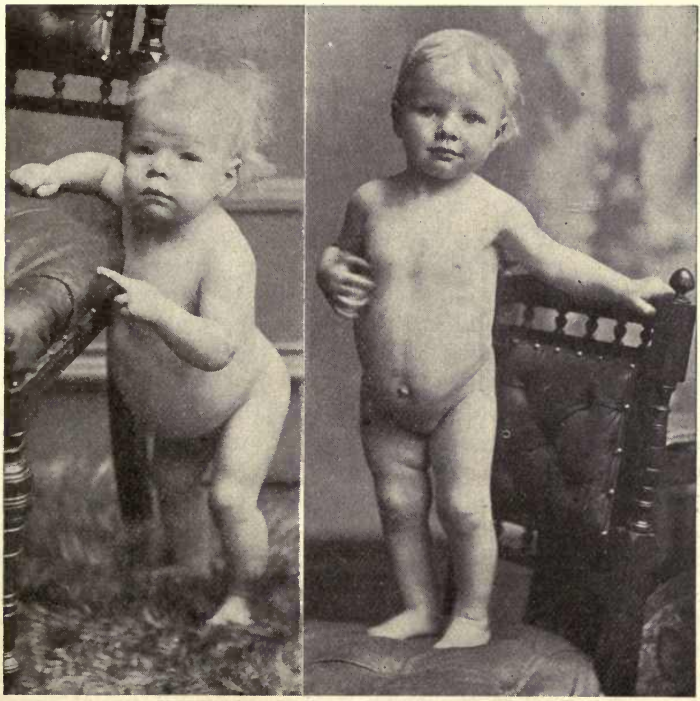


FIG. 112.—Diagram showing the position of the thyroid gland. *TC*, thyroid cartilage; *TG*, thyroid gland; *T*, trachea. The parathyroids are indicated in black.

The Thyroid Gland.—The thyroid gland consists of two lobes which are connected with one another by a narrow bridge of tissue. They are nearly equal in size and measure about 5 cm. in length. Their combined weight is 30 grams. In man they assume a position in close relation with the trachea, at its junction with the cricoid and thyroid cartilages of the larynx. Their substance is composed of a large number of acini, containing in their interior a viscous colloid material. It is supposed that this material finds its way into the adjoining lymph channels. It is also of importance to note that their substance embraces four small bodies, the cells of which present certain characteristics which clearly differentiate them from the surrounding mass of the thyroids. These structures form the so-called *parathyroid gland.*

In a general way, it may be said that man is subject to

either an increased or a decreased output of anyone of the endocrine products. Either condition usually gives rise to a complex of perfectly definite symptoms. In the case of the thyroid, it has been established by clinical studies that a lowered production of its active principle leads to *cretinism*



A B

FIG. 113.—Cretin before (A) and after (B) treatment with sheep's thyroid. (*Nicholosn.*)

and *myxedema*. The former is a deficiency disease of infancy, and the latter a disease of adult life. Cretinism or infantilism means that the infant is dwarfed in its stature, owing to a retardation in the growth of its bones and soft parts. The face presents a swollen appearance; the features are imperfectly outlined; the hair is scanty and the skin thick and

dry. Mentally, the cretins are far behind children of the same age. This condition may readily be remedied in the course of a few weeks by the careful administration of extract of thyroid. Very similar symptoms may develop in adults, giving rise to the condition of myxedema. These symptoms also yield to the feeding of thyroid substance.

Too copious a production of thyroid secretion gives rise to an extreme irritability of the nervous system, trembling of the muscles, and psychic exultation. When these symptoms finally become associated with attacks of tachycardia or palpitation of the heart and bulging of the eyes or exophthalmos, a distinct clinical picture is produced which is commonly termed *Basedow's disease* or *Grave's disease.* While this functional disturbance usually leads to the death of the patient, if allowed to develop fully, it may be remedied soon after its onset by the partial excision of the thyroids. About one-third of the total substance of these organs must always be left behind, because the removal of too large a portion is invariably followed by death.

It is to be noted, however, that the thyroids need not be markedly enlarged, although yielding excessive amounts of secretion. Contrariwise, it is a well known fact that those persons who are afflicted with *goiter* or enlarged thyroids, need not present symptoms indicative of a superfluous secretion of thyroid. In most instances the development of a goiter merely suggests an unusual growth of the framework of this gland, which often seriously interferes with the flow of the respiratory air.

These clinical studies, as well as animal experimentation, have shown that the thyroid furnishes an internal agent which plays an important part in the *metabolism* of the tissues, chiefly those of the nervous system. The product of the parathyroids is concerned with the elimination of certain toxic substances formed in the course of metabolism. When these glandular structures are removed, these substances accumulate in the system and finally produce the clinical picture of *tetany*, consisting of muscular tremors and spasms as well as of a loss of the tonus and coördination of the skeletal musculature.

The Adrenal Glands.—These small pea-shaped organs are situated one above each kidney (Fig. 114). They are supplied by several minor branches of the aorta and pour their venous drainage into the suprarenal vein, a tributary of the inferior vena cava. It has been established that their total removal leads to the death of the animal within a few days, while the extirpation of only one organ does not. Likewise, it is possible to remove one gland and to transplant

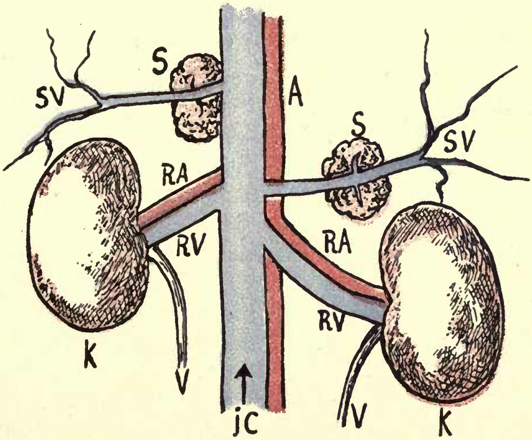


Fig. 114.—Diagram to illustrate the position of the adrenal glands (rabbit). *K*, kidneys; *V*, ureters; *R V*, renal veins; *RA*, renal arteries; *JC*, inferior vena cava; *A*, abdominal aorta; *S*, adrenal glands; *SU*, suprarenal veins. In man, the two kidneys lie very nearly in the same horizontal plane; in fact, the right organ frequently below the left.

the opposite one into some other region of the body without producing fatal results. These facts clearly prove that these bodies furnish an internal product which is absolutely essential to the life of the animal. This conclusion finds additional support in the clinical picture presented by persons suffering from *Addison's disease*. It has been established that the degeneration or destruction of these bodies in man gives rise to muscular weakness and tremors, convulsions, and a decided bronzing of the skin. This disease usually proves fatal within a few months.

The chief function of the adrenal glands consists in the production of an agent which constricts the bloodvessels. It is known as *adrenin.* This drug-like body is secreted by the medullary portions of these glands and is then passed into the suprarenal veins, whence it reaches the venous circulation. On being eventually diverted into the arteries and arterioles, it causes the smooth muscle fibers of these channels to contract. It need scarcely be mentioned that this constriction of the arterioles retards the escape of the arterial blood into the capillaries and gives rise to an increase in the arterial bloodpressure.

In accordance with this characteristic action of adrenin, it is believed that these glands constantly secrete minimal amounts of this agent which thus tend to retain the bloodvessels in a condition of semi-constriction or tonus. A more copious outpouring, however, may result at any moment in consequence of reflex stimuli. Thus, it has been stated that its output is considerably increased during emotional states, induced by fear and anger. In consequence of this increased production of adrenin, larger amounts of sugar are mobilized which find their way into the urine, thereby establishing the condition of emotional glycosuria.

The active principle adrenin is usually obtained by macerating these glands and extracting them in normal saline solution. This extract is then injected into the bloodstream. The commercial preparation of it, which is known as *adrenalin,* is employed to stop bleeding, because when applied to an injured surface, it constricts the opened vessels, thereby diminishing the flow of the blood. While this action is only temporary, it usually lasts a sufficient length of time to allow coagulation to set in. The bleeding points are then blocked in a more effective and permanent manner. It might also be mentioned that adrenalin tends to overcome muscular fatigue, because it intensifies the entire circulation. Its medicinal use for this particular purpose, however, is contra-indicated physiologically.

The Liver and Pancreas.—Repeated mention has been made of the fact that the sugar of the portal blood is stored in the cells of the liver in the form of glycogen, and that this

animal-starch may again be converted into circulating sugar by these cells. It is assumed, therefore, that the liver produces an inherent agent to which these chemical changes are assigned. Likewise, it has been stated that the cells of the islands of Langerhans of the pancreas furnish an internal secretion which changes the circulating sugar into a form adapted to the chemical powers of the tissue cells. Sugar which has not been acted upon in this way, cannot be oxidized so readily and must, therefore, remain behind in the blood and eventually be excreted by the kidneys. This metabolic disturbance is one of the fundamental causes of diabetes mellitus.

The Pituitary Gland.—This structure lies at the base of the brain, occupying here a recess in the sphenoid bone. It appears as a reddish-gray mass of about the size of a pea, and is connected with the main mass of the cerebrum by a peduncle. It consists of two principal portions which are designated respectively as its anterior and posterior lobe. The former appears to be connected in some way with the metabolism of the bones, this conclusion being based upon the fact that the pituitary is usually enlarged in all cases of *giant growth* or *acromegaly.* This form of gigantism affects the bones of the face as well as those of the fingers and toes, rendering them club-shaped and frequently causing a general contortion of the part. Accordingly, it is thought entirely probable that the unusual length of the long bones of giants finds its cause in an excessive production of this particular hormone. Contrariwise, a diminished secretion of this active principle must retard the growth of the bones, and give rise to the condition of *dwarfism.*

The posterior lobe of the pituitary consists of a tissue which bears a close resemblance to the framework of nervous tissue. It does not seem to possess a specific function. That portion of the posterior lobe, however, which lies in contact with the anterior lobe, consists of a row of lining cells possessing a true secretory character. When injected into the bloodstream, the extract of this particular segment of the pituitary gland evokes a constriction of the blood-vessels and rise in the arterial pressure very similar to that

noted after the administration of adrenalin. Repeated experimentation has shown that the hormone secreted by these cells possesses a stimulating action upon the smooth muscle tissue throughout the body and also excites secretion; for example, that of milk.

The Thymus.—This organ occupies a position at the base of the heart and in front of the great vessels. The size of this organ differs considerably in accordance with the age of the person. In infants, for instance, its average weight is 12 grams, at puberty 35 grams, and at sixty years less than 15 grams. Relatively speaking, therefore, it is much larger early in life than after puberty. Its structure is similar to that of lymphoid tissue and shows a division into a cortical and medullary portion.

Regarding the function of this organ very little is known. It is obviously metabolic in its function, attaining its greatest importance at the time of puberty. Inasmuch as it atrophies during adult life, it is supposed to be connected with the development of the sexual organs and characteristics.

The Spleen.—While it has been proven that the spleen does not furnish an internal secretion, its function is as yet so much in doubt that great difficulty is experienced in classifying it in its proper relation to other structures. It is situated somewhat below and toward the left side of the stomach and possesses a flat, elongated outline. Its blood-supply is furnished by the splenic artery, a branch of the cœliac axis of the abdominal aorta, while its venous drainage is conveyed into the portal vein. When its capsular sheath is removed, it will be found that partitions of connective tissue or trabeculæ enter its interior and subdivide the entire organ into a number of spaces which are filled with spongy material, called the *spleen-pulp*. The meshes of the pulp are occupied by red and white blood corpuscles as well as by large giant cells, possessing amœboid qualities. The organ as a whole presents the characteristics of lymphoid tissue, such as forms the principal mass of the lymphatic glands.

Inasmuch as this organ may be removed without serious consequences, it may be concluded that it does not furnish a

specific internal secretion. Furthermore, the fact that it is not indispensible to the life of the animal, leads us to suspect that its function may be transferred at any time to other organs. Its lymphoid structure brings to our minds first of all the possibility that it forms white blood corpuscles. But, since lymphoid tissues in general are engaged in this process, the removal of this organ merely causes the other tissues of like character to compensate for this loss.

The spleen is also one of the organs in which the red blood corpuscles are destroyed. This conclusion is based upon the fact that the splenic pulp is loaded with fragmented red cells. It should be remembered, however, that this organ is not the only place in which these corpuscles are destroyed. A far more important destructive power is possessed by the liver. Thus, it is commonly believed that the spleen merely instigates the disintegration of the senile red corpuscles, permitting the liver to reduce them further into their elementary constituents. It has been noted in a preceding chapter that the pigments of the bile as well as the iron are derived from these cells.

Owing to the spongy character of the substance of the spleen, allowing this organ to become highly distended, it has also been thought that it serves as a sort of reservoir for the portal blood. Thus, it is believed by some physiologists that it accommodates varying amounts of blood, thereby giving rise to a more equal distribution of the blood when required for purposes of digestion.

PART V

THE NERVOUS SYSTEM

CHAPTER XXX

THE FUNCTIONAL DEVELOPMENT OF THE NERVOUS SYSTEM

The General Arrangement of the Nervous System.—The many millions of neurones composing the nervous system, are moulded into complex masses of tissue, the minute arrangement of which can only be thoroughly understood after considerable study. In general, however, it may be stated that the nervous system consists of a central and a peripheral part. The central one embraces the cerebrum, cerebellum, basal ganglia, medulla oblongata, and spinal cord, while the peripheral one is composed essentially of an intricate network of nerves and a large number of ganglia. Twelve pairs of these nerves are given off from the cerebrum and the region of the pons and medulla, while thirty-one pairs arise from the spinal cord itself.

The peripheral extent of the nervous system also embraces numerous nerve fibers and ganglia which control the functions of the viscera and are not under the control of the will. They form what is known as the *autonomic nervous system*. Hence, it will be seen that the nervous system may also be divided into a cerebrospinal part and an autonomic part. The former embraces the aforesaid central masses of nerve tissue as well as the twelve pairs of cranial and thirty-one pairs of spinal nerves. Correspondingly, the latter is made up of: (*a*) a number of ganglia and nerves which are situated along the thoracic division of the spinal cord, and (*b*) a number of ganglia and nerves located along the cranial

nerves and sacral segment of the spinal cord. For this reason, it is usually stated that the autonomic system belongs to the peripheral nervous system and is composed of a *sympathetic* and a *parasympathetic* division. The following outlines may be of service in understanding this classification:

- Nervous system
  - Central
    - Cerebrum
    - Cerebellum
    - Basal ganglia
    - Medulla
    - Spinal cord
  - Peripheral
    - Cranial nerves
    - Spinal nerves

- Nervous system
  - Cerebro-spinal (medullated)
    - Cerebrum
    - Cerebellum
    - Basal ganglia
    - Medulla
    - Spinal cord
    - Cranial nerves
    - Spinal nerves
  - Autonomic (non-medullated)
    - Parasympathetic ramifications and ganglia from the cranial and sacral spinal nerves.
    - Sympathetic ramifications and ganglia from the dorsal spinal nerves.

The General Function of the Nervous System.—The many millions of cells composing the body of the higher animal, work in groups, each fulfilling a particular purpose in order to achieve a functional whole. Hence, the body may be likened to a large manufacturing establishment, in which each department turns out its own particular contrivance to be later on joined with others into a complex piece of machinery. In order to effect a harmonious and purposeful working of these different departments, a close correlation must be established between them through foremen who in turn are directed by a manager.

Many parts of our body, and principally those subserving the vegetative processes, are able to act independently of one another, but the best results can only be obtained if the

functions of the different organs are correlated to yield a common general product. For this reason, nerve centers and nerve paths have been established through which the different constituents of the body are enabled to exchange impulses signifying their needs to the governing body of the entire mechanism. Likewise, impulses may in this way be relayed to them informing them about the functional requirements of other parts. The neurones accomplishing this coördination, are always arranged in such a way that their conductile elements form definite paths or *nerves*, while their generating parts or cell-bodies are combined into *nuclei* and *centers*. Thus, we may justly draw the general conclusion that the central nervous system is the seat of many centers controlling the actions of the peripheral parts, while the nerves merely serve the purpose of bringing the latter into functional relation with the former.

The different parts of our body must accomplish the right things at the proper time. When a muscle contracts it is made to do so by a nerve impulse conveyed to it from its center. Furthermore, its contraction must be *coördinated* with those of other muscles, otherwise a *purposeful* action cannot be obtained. The same statement may justly be made regarding other organs. Thus, we have seen that the flow of the digestive secretions is accurately timed so as to permit them to act upon the foodstuffs in proper order. Likewise, the calibre of the bloodvessels is invariably adjusted in a way to correspond to the energy of the heart, otherwise the normal height of the bloodpressure cannot easily be retained. Quite similarly, the bloodpressure is altered repeatedly so as to agree with the varying states of activity of the different organs.

The Simple Nervous System.—Attention has already been called to the fact that the structural unit of the nervous system is the neurone, and that the most elementary nervous action or reflex requires the presence of at least two neurones. One of these conducts from the periphery to the center, and the other from the center to the periphery. The former is known as the afferent or sensory neurone and the latter, as the efferent or motor neurone. Both are functionally

related to one another by the synapse, and both together constitute what is known as a reflex circuit.

These reflex circuits are first noted in the coelenterates. Below this species nervous elements are not discernible, although even these organisms show various motor reactions in consequence of stimuli. These reactions, however, cannot be called reflexes, because they are accomplished solely by conduction through ordinary protoplasm. The name commonly applied to them is reflex-like reactions. Thus, it will be seen that the animals may be divided into two classes: namely, those possessing and those not possessing nervous tissue. The former exhibit simple reflexes as well as volitional reactions and the latter, solely reflex-like reactions.

We are now chiefly concerned with those animals whose functions are correlated by nervous tissue. Even a very casual study will show that these animals may in turn be divided into two groups: namely, those exhibiting only simple reflex actions, and those presenting in addition complex volitional responses. Thus, if we contrast an earthworm with a mammal, it will be evident that the former is a simple reflex animal and absolutely devoid of psychic activities, whereas the behavior of the latter is dominated by volition. This statement, however, is not meant to imply that the mammal does not present simple reflexes, but solely that its reflex life is amplified by associations and their consequent motor reactions. In other words, the simple reflex life of the lower forms is dominated in the higher animals by certain psychic products.

The Segmental Animal.—Reflex action may be studied best in such animals as the vermes and crustaceæ. Especially the former display a typical segmental arrangement, *i.e.*, their bodies are composed of a number of segments which are in possession of separate organs. Thus, each portion of their body may lead a practically independent existence, although all are under the control of a head-ganglion or "brain" which causes their separate actions to be correlated for the attainment of a common purpose.

Each segment contains a number of reflex circuits, the synapses of which are situated centrally. In this way, a

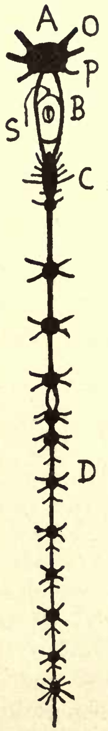


Fig. 115.—Diagrammatic representation of the nervous system of the crayfish. *A*, supraesophageal ganglion; *B* commissure; *C*, subesophageal ganglion; *D*, first abdominal ganglion; *O*, optic nerve; *P*, antennary nerve; *S*, stomatogastric nerve.

main ganglion is formed which serves as the controlling agent of each segment. These ganglia are connected with one another by longitudinal neurones which thus establish communication between them as well as with the head-ganglion or "brain." These interganglionic fibers form the beginning of the spinal cord of the higher animals. The chief purpose of this structure is that of a highway connecting the brain with peripheral parts.

The essential points of this discussion may readily be reviewed with the aid of Fig. 115 which represents the nervous system of the crayfish, schematically outlined. It consists of thirteen ganglia, six of which belong to the abdomen, six to the thorax, and one to the head. Each ganglion controls the corresponding portion of the body, and communicates with the neighboring ganglia as well as with the head-ganglion. The latter receives diverse sensory impressions from the receptors for sight, hearing, and touch, and is thereby enabled to exert a much greater influence upon the animal as a whole than the other ganglia.

The Development of the Association Realms. Volition.—While this simple reflex system is also present in the higher animals, it has been considerably amplified by the development of an additional number of neurones which subserve psychic activities. For the present, these higher activities may be designated in brief as *associations*. In the earthworm or crayfish an impact upon the integument gives rise to a musculo-motor reaction without involving volition or similar psychic processes. The same direct course is followed by those afferent stimuli which ascend from the retina of the eye or the organ of hearing.

In the higher animals, these simple reflex

processes are subordinated to the activities of the association centers, situated in the more recently developed cerebrum. The outer realm or cortex of this structure embraces a large number of ganglion cells which are set aside for the purpose of associating many sensory impulses before they are actually allowed to pass on to the motor end-organs. In this way, it is made possible to activate a certain effector not only in a reflex way but also volitionally. When the cornea of the eye is touched, the eyelids are closed in order to protect the eyeball against injury. This act is non-volitional in its nature and is, therefore, a simple reflex. But, it is also possible to close the eyelids volitionally in consequence of certain associations formed in the corresponding center of the cerebrum. Likewise, an intense sound or other sensory impression may lead either to an almost instantaneous protective muscular reflex, or may first be relayed into the corresponding association center in the cerebrum to undergo certain modifications. In the latter instance, it may be inhibited or may be permitted to effect a motor response of a more complex and purposeful character. In other words, it is then closely dominated by volition.

Naturally, the development of the cerebral association areas places the animal upon a level considerably above that occupied by the simple reflex animals. It is to be noted, however, that this development takes place gradually, its beginning being noted in the reptilia and amphibia and its highest stage in man. Thus, we find that the simple reflex system of the frog and turtle has been amplified by the formation of a relatively small cerebrum, the principal part of which is occupied by the association center for smell, the olfactory lobes. Since the existence of these animals is closely dependent upon their purposeful behavior towards these sensations, it cannot surprise us to find that they are placed in a particularly favorable position to analyze them.

Another important complex of nervous tissue is the hind-brain or cerebellum. It may be stated at this time that this organ serves to coördinate the different muscular movements, so that they may be executed with precision and in harmony with one another. Even a casual observation will show that

the amphibia and reptilia are not greatly in need of associations of this kind, because their movements in space are static in character. They move sluggishly along straight lines. Thus, it is found that the cerebellum of the frog and turtle is rudimentary in size and structure. Contrariwise, the cerebellum of the birds presents a high stage of development, because these animals must be able to coördinate their muscular movements very precisely in order to retain their equilibrium and to be able to orient themselves in space.

CHAPTER XXXI

THE SPINAL REFLEX ANIMAL

The Development of the Spinal Cord.—It has previously been emphasized that the ganglia of the different portions of the segmental animals are connected with one another by longitudinal axones which thus form a nerve cord traversing the body in a direction from before backward. A similar arrangement is present in the mammals. These animals are in possession of a number of simple reflex centers which are arranged in series and are connected with one another by longitudinal bundles of nerve fibers. Accordingly, there are deposited along the dorsal aspect of these animals numerous ganglion cells which are united not only with the peripheral motor and sensory organs but also with one another. Admittedly, therefore, the basis of the rudimentary spinal cord is formed by neurones subserving simple reflex activities.

The subsequent development of the forebrain and hind-brain necessitates the addition to this reflex system of numerous neurones which connect the spinal ganglion cells with those constituting the cerebrum and cerebellum. Thus, there is built up upon this *local reflex mechanism* of the cord a second one which bears the characteristics of a long-conduction system. The latter establishes communication not only between the brain and the different reflex centers of the spinal cord, but also between the brain and the distant motor and sensory organs. The neurones effecting this long distance conduction, form the so-called *projection system.* Hence, the spinal cord of the higher animals differs from that of the lower forms chiefly in that it contains numerous afferent and efferent projection axones as well as many ganglion cells establishing relay stations for these fibers.

It has been mentioned in one of the preceding chapters that the distance between the cerebrum and the motor end-

organs, such as the muscles of the foot, is usually covered by two efferent neurones arranged in series, while the corresponding sensory path is generally formed by three consecutive afferent neurones. It is also to be noted that the connections between the sensory and motor end-organs situated in the region of the head, are established in a direct way by twelve pairs of cranial nerves. The last six of these enter the cerebro-spinal tract in the region of the medulla oblongata, whereas the first six, such as the nerves of smell and sight, enter the brain above this structure.

The Spinal Cord.—The spinal cord of man appears as a cylindrical structure, measuring from 40 to 45 cm. in length,

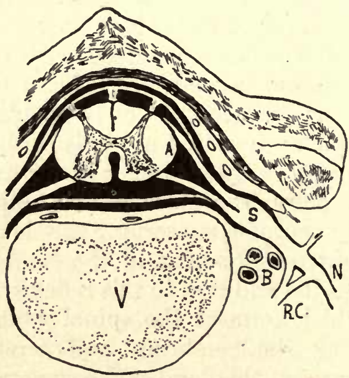


FIG. 116.—Transverse section through the region of the fourth cervical vertebræ. *V*, body of vertebra; *B*, vertebral blood-vessels; *N*, spinal nerve; *RC*, ramus communicans; *S*, spinal ganglion; *A*, subarachnoidal space investing spinal cord.

and 12 mm. in diameter. It is contained in the *vertebral canal*, which is formed by the bodies and laminæ of the successive vertebræ. It is enveloped by membranes, fatty tissue, and lymph. Next to the bony wall of this canal lies the *dura mater*, a tough fibrous membrane, serving as the periosteal lining of these bones. Then follows the *arachnoid*, and lastly, the *pia mater*. The arachnoid is a delicate membrane which lies in rather close contact with the dura, but is in many places widely separated from the pia. These sub-

dural and subarachnoid spaces are filled with a lymph-like fluid which possesses the general character of cerebro-spinal liquid.

Beginning at the level of the atlas, the spinal cord gives off thirty-one pairs of nerves, or, in general, one pair for each vertebra. These nerves leave the vertebral canal through

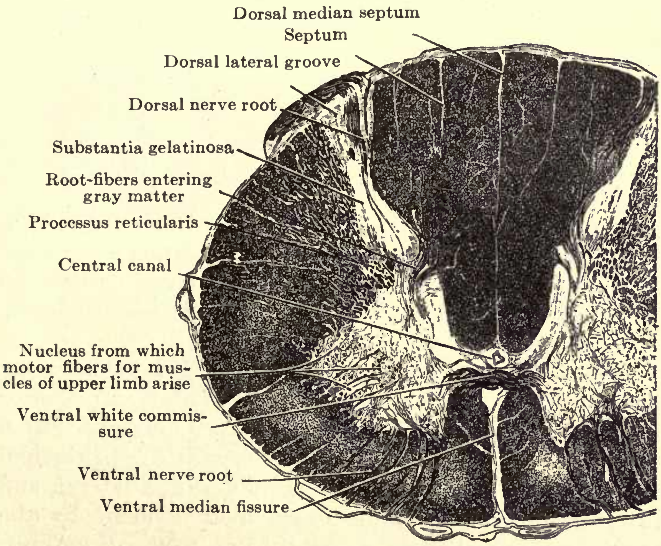


FIG. 117.—Cross-section through the human spinal cord at the level of the fifth cervical nerve, stained by the method of Weigert-Pal, which colors the white matter dark and leaves the gray matter uncolored. (*From Cunningham's Anatomy.*)

apertures between the vertebræ, which are called *intervertebral foramina.* The adult spinal cord, however, does not occupy the entire length of the vertebral canal, but terminates opposite the second or third lumbar vertebra. Below this point are found a number of nerve fibers which tarry in the wake of the cord before they actually leave this canal. This bundle of fibers forms the *filum terminale.*

If a cross-section is made of the spinal cord, it will be found to embody a darker central mass of gray matter and a lighter

marginal zone of white matter. The former presents itself as two crescent-shaped masses which are connected with one another by a narrow bridge or commissure. For this reason, it exhibits an outline similar to that of the letter H. The white matter surrounds this central core of gray substance on all sides in the form of a relatively narrow capsule.

Before proceeding further brief reference should be made to the fact that this peculiar appearance of the cross-section of the spinal cord is occasioned by differences in the arrangement of its neurones. *Gray matter* consists essentially of the cell-bodies of the neurones and their central processes, while *white matter* embraces chiefly axones enveloped by their medullary sheaths. Accordingly, it will be seen that the outer zone of the spinal cord is made up almost exclusively of nerve fibers conducting impulses in a longitudinal direction through the cord, while the cells of the central gray matter serve as relay stations for these impulses, enabling them to leave this structure at any level to reach the corresponding segment of the body.

The Spinal Cord as an Organ of Conduction.—The cross-section of the spinal cord presents an anterior and a posterior fissure, which divide this entire area incompletely into a right and a left half. Each half presents three principal columns of white matter: namely, an anterior, a lateral, and a posterior. This division is made more evident by the fact that each spinal nerve arises by two *roots*, an anterior and a posterior. The fibers of the former pierce the white matter between the anterior and lateral columns, and the latter, between the posterior and lateral columns.

This anatomical arrangement coincides very closely with the functional character of the nerve fibers composing these columns of white matter. Thus, it may briefly be stated at this time that the spinal cord possesses two chief functions: namely, that of *conduction*, and that of a *center for reflex action.* If we confine ourselves for the present to its function as a highway for nerve impulses, it should be emphasized that its white matter is made up of two sets of fibers, one of which connects its successive segments with one another and one which establishes communication between the brain and

distal parts. Both sets embrace afferent as well as efferent axones.

If we regard this subject-matter in a very general way, it may be stated that those fibers which are concerned with reflex action, occupy a position next to the gray matter, while those belonging to the projection-system are arranged as definite outer bundles. Secondly, those fibers which

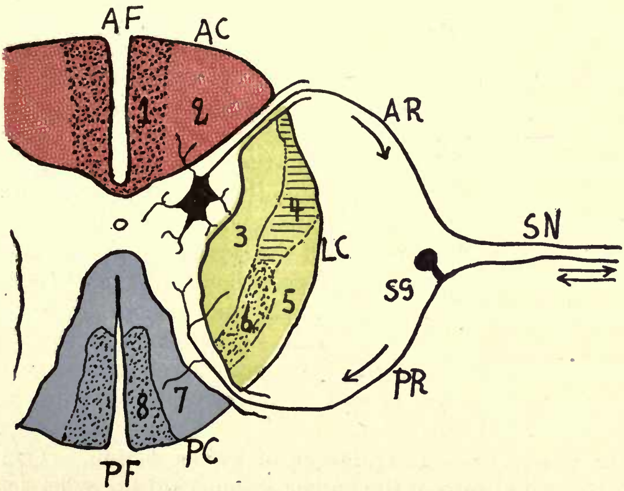


FIG. 118.—Conduction in the spinal cord. *AF*, anterior fissure; *PF*, posterior fissure; *AC*, anterior column; *LC*, lateral column; *PC*, posterior column; 1, direct pyramidal tract; 2, anterior ground bundle; 3, lateral ground bundle; 4, Gower's tract; 5, Flechsig's tract; 6, crossed pyramidal tract; 7, column of Burdoch; 8, column of Goll; *AR*, anterior root; *PR*, posterior root; *SG*, spinal ganglion; *SN*, spinal nerve.

conduct in an afferent direction, occupy chiefly the posterior column and to some extent also the lateral column. Contrariwise, those fibers which convey impulses in an efferent direction, descend through the anterior column and in a measure also through the lateral column. It is to be noted, therefore, that the white matter of the spinal cord is subdivided into distinct bundles of nerve fibers subserving conduction in special directions. These tracts are either afferent (ascending) or efferent (descending) in their character.

This division of function is in entire agreement with the localization of conduction exhibited by the *roots of the spinal cord*. The fibers leaving the cord in front are efferent, which implies that the cell-bodies of these neurones are situated in the *anterior segment or horn of the gray matter*, while their axones pursue a course outward through the *anterior root*. Contrariwise, the fibers forming the *posterior root*, conduct in an afferent direction. Their cell-bodies are situated near the junction of the anterior and posterior roots, where they form a small nodule which is designated as the *spinal ganglion* (Fig. 118). Distally to this point, the fibers of the posterior root intermingle with those of the anterior root, forming the spinal nerve proper. Centrally to the spinal ganglion, however, the afferent fibers pursue a separate course and finally enter the *posterior realm or horn of the gray matter*. Those impulses which are to be conveyed to higher levels of the cord and the cerebrum, are transferred to the ascending fibers of the posterior tracts, and those intended for the cerebellum, to the corresponding ascending lateral tracts. It need scarcely be emphasized that these afferent fibers are derived from peripheral sense-organs or receptors, while the efferent fibers eventually terminate in motor-organs or effectors.

The Spinal Cord as an Organ of Reflex Action.—The fact that the spinal cord of the higher animals aids in reflex action, may readily be proved by removing the brain of an etherized frog, and by subjecting this brainless animal later on to stimulations. In accordance with the preceding discussions, it must be evident that the destruction of the cerebral association centers converts this animal into a reflex machine which is incapable of perceiving pain and of receiving any sensory impulse in "consciousness." The ordinary afferent and efferent impulses, however, are not destroyed, excepting those which in part traverse the higher segments of the nervous system.

If the foot of such a "reflex frog" is stimulated by immersing it in very dilute acetic acid or by pinching it slightly with the forceps, the muscles of this leg contract. The foot is then removed from the seat of the stimulation. This reaction

follows after an appreciable interval, which becomes the shorter the stronger the stimulus. The time intervening between the moment of the application of the stimulus and the muscular reaction, is called the *reflex-time.*

It is also to be noted that a somewhat greater strength of stimulus eventually evokes movements of the opposite hind-leg, abdominal parts, and fore-legs. This result leads us to infer that a strong stimulus involves not only the reflex circuits of the leg stimulated, but also those in adjoining parts of the body. This phenomenon is designated as *spreading of impulses* or *spreading of reflexes.* It may also be evoked by increasing the irritability of the nervous system as a whole. A drug commonly used for this purpose is strychnin, which is believed to establish a more intimate connection between the sensory terminals and dendrites of the motor neurone. Because of this change in the synapses, the sensory impulses are enabled to influence a much greater number of motor neurones. Thus, it is a well known fact that even the slightest mechanical stimulus applied to the skin of a frog poisoned with strychnin, will give rise to very extensive and prolonged muscular spasms.

All these reflex contractions of the muscles cease immediately after the spinal cord has been destroyed. This result prompts us to conclude that this structure is absolutely essential for these reflex responses, because it contains the synapses of the afferent and efferent neurones concerned in these reactions. For this reason, it is commonly stated that the cord is an important seat of reflex activity. It should be noted, however, that it is not the only part of the nervous system set aside for this function, because reflexes may also be obtained in the domain of the cranial nerves, as well as in that of the sympathetic nervous system.

In the amphibians and reptilians it is also evident that these spinal reflex centers are localized in particular segments of the cord. Thus, it may readily be proved by destroying different portions of the spinal cord of the frog that the reflexes evoked from the hind-legs, are controlled by ganglion cells which are situated opposite the seventh and eighth vertebræ. Quite similarly, it may be shown that the synap-

ses of the neurones concerned with the reflex responses of the fore-legs, are placed opposite the third and fourth vertebræ. In locating these centers, it should be remembered that the spinal column of the frog consists of only nine vertebræ. The tenth vertebra is modified to form the dorsal wall of the very extensive pelvis. The point of union between these two vertebræ lies at the prominence upon the dorsal aspect of the body of this animal.

While it may be granted that this localization of reflex function is not so evident in the higher animals as in the lower, it is nevertheless quite obvious that the spinal cord of the former embraces a number of simple centers which are concerned with the processes of micturition, defecation, and reproduction. Besides, this structure displays a distinct segmental arrangement, because each spinal nerve is apportioned very nearly to that segment of the body which lies opposite its origin. The lowest nerves, however, bend back considerably in order to reach the posterior parts of the body. This arrangement is clearly portrayed by the sciatic nerve, the nucleus of which lies in the lumbar segment of the spinal cord, while its fibers pass almost directly backward.

Examples of Reflex Action.—By means of the sciatic nerve it is possible to evoke a reflex which is no doubt familiar to every one. It is termed the *patellar reflex*, and is elicited by tapping upon the patellar ligament, while the leg is suspended across the edge of a chair or table. The impulses so generated in this locality, are conveyed to the sciatic center, and thence outward to the quadriceps femoris muscle. On contracting, this muscle extends the leg upon the thigh. The varying intensity of this reflex permits us to form an idea regarding the state of irritability of the entire nervous system, and to locate lesions of its constituent parts. Injuries to the cord frequently abolish this reaction entirely, while lesions of the higher centers increase its intensity.

It would be incorrect, however, to gain the impression that reflexes invariably consist of movements. Thus, we have previously noted that the flow of saliva, gastric juice and pancreatic juice is the direct result of stimuli brought to bear upon the secretory elements of these glands. We have also

become acquainted with the reflex character of the acts of sneezing and coughing, the closure of the eyelids, vomiting, the dilatation and constriction of the pupil, the erection of the hairs, and the changes in the caliber of the bloodvessels. All these reactions are not dominated by the will, and are, therefore, reflex in character.

Perception Reflexes.—The importance which is usually attached to those reflexes which are evoked with the aid of the spinal cord, may have led us to believe that this structure is practically the only one mediating these reactions. This is by no means true, because many impulses subserving reflex action never enter the spinal cord, but remain confined to the sympathetic system or certain tracts of the basal portions of the brain. Thus, it is possible to elicit a secretion of gastric juice by local stimulation even after the stomach has been separated from the central nervous system by the division of all its connecting paths. Very similar results may be obtained with the intestine and urinary organs. These facts prove that the autonomic nervous system is in possession of many local reflex centers which are capable of acting independently of central parts and require the latter only when a correlation of function is essential.

Several of the reflexes afore-mentioned actually involve tracts and centers which might rightly be said to belong to the cerebrum. But, since these impulses are not controlled by volition, they must nevertheless give rise to simple reflex acts. In fact, several reflexes must first be qualified by the element of perception before they can attain their full development. Thus, it has been mentioned above that a secretion of saliva and gastric juice usually follows the reception of impressions of smell, taste, and sight without local stimulation of these glands. These reflexes embodying a distinct psychic element, are known as *perception or association* reflexes. Likewise, the entrance of a larger particle of dust into the conjunctival sac calls forth a copious secretion of lacrimal fluid. This is a pure reflex. But, a copious flow of lacrimæ may also result in consequence of certain emotional concepts. In the latter case, this reaction possesses the character of a perception-reflex.

CHAPTER XXXII

THE BRAIN

The General Arrangement of the Brain.—The brain occupies the cavity of the cranium, which is formed by the union of eight plate-like bones: namely, the frontal, two parietal, occipital, two temporal, sphenoid, and ethmoid. It consists of several parts, the largest of which are the forebrain or cerebrum and the hindbrain or cerebellum. Upon the under surfaces of these structures are found several smaller masses of nerve tissue, namely, the optic tract, pituitary body, corpora quadrigemina, and the pons and medulla oblongata. The two structures mentioned last constitute the connecting bridge between the cerebrum and the spinal cord. They are arranged in the form of a stem around which the higher parts are moulded.

The enveloping membranes of the brain bear the same names and present the same general appearance as those investing the spinal cord. Directly within the inner plate of the cranial bones lies the dura mater, and next to it, the arachnoid. Between the latter and the pia mater are found numerous spaces which frequently acquire a considerable size and are filled with a lymph-like fluid, bearing the characteristics of the general cerebro-spinal liquid. The pia follows the surface of the brain very closely, dipping into all its furrows, while the dura and arachnoid do not.

The central nervous system of the higher animals is not a solid mass of tissue, but gives lodgment to numerous spaces and channels which are filled with cerebro-spinal fluid. This system begins in front with the lateral ventricles, the walls of which are formed by the cerebrum or forebrain. As is indicated in Fig. 119, these spaces communicate with the third ventricle which is situated within the narrowed part constituting the "'tween-brain." Then follows the aqueduct

of Sylvius within the mid-brain, and lastly, the fourth ventricle surrounded by the cerebellum or hindbrain. The channel then narrows into a tube which traverses the entire spinal cord about midpoint between its anterior and posterior fissures.

All these spaces contain a lymph-like fluid which is known as cerebro-spinal liquid and originates in a glandular structure of the cerebral ventricles, called the *choroid plexus.* The composition of this medium is very similar to that of

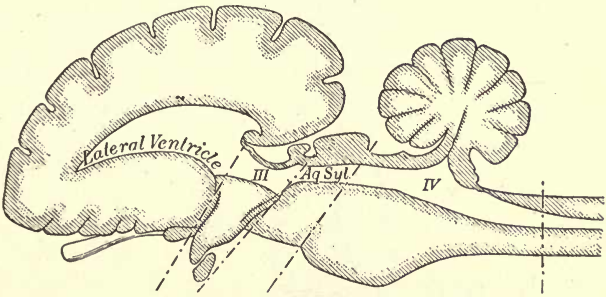


Fig. 119.—Diagrammatic median longitudinal section of a mammalian brain. (*Edinger.*)

the fluid filling the subdural and subarachnoid spaces. Sufficient evidence is at hand to show that all these passages communicate with one another, and that the cerebro-spinal fluid is finally drained off through the lymphatic ducts of the head and the large veins of the cranium. The latter receive at frequent intervals minute nipple-like projections from the arachnoid which are termed *Pacchionian bodies.* These small membranous saccules are suspended in the bloodstream, thereby bringing the subarachnoidal fluid into diffusion relation with the venous blood. While these projections serve as natural outlets for the lymph, the process by means of which the latter enters the blood is not one of simple filtration.

The Simple Brain.—In order to be able to obtain a concise idea regarding the structure of the complex brain of the mammals, it seems best to initiate this subject-matter with a

brief study of the simple brain of the frog (Fig. 120). The cranial cavity of this animal is situated well forward between the eyes. On opening it two white, hemispherical masses of nerve tissue are brought into view which jointly constitute the *cerebrum*. Farther forward lie two long, bulbular masses of tissue which are termed the *olfactory lobes*. Attention has already been called to the fact that the movements of these animals are controlled chiefly by the sense of

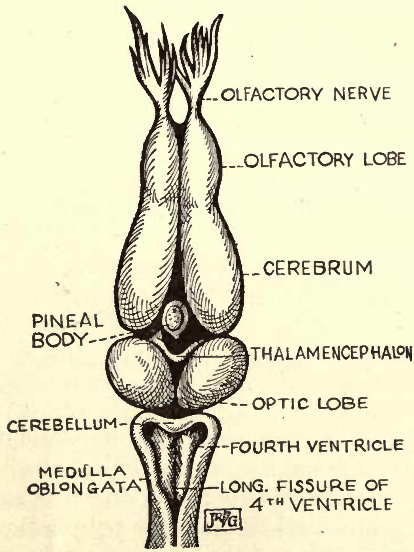


FIG. 120.—The brain of the frog.

smell. For this reason, we find that their cerebrum is very largely taken up by the "association center" pertaining to this sense.

The 'tweenbrain, midbrain and hindbrain of the frog and allied animals present a very rudimentary development, which again is in entire agreement with their mode of life. They move very sluggishly and progress principally along straight lines without executing rotary motions. Since the cerebellum gives rise to co-ordinated muscular movements,

it will, therefore, be seen that it need not be highly developed in these animals. The reverse condition prevails in the birds, while the mammals occupy in this regard an intermediary position.

Back of the 'tweenbrain lie two grayish, rounded masses of nerve tissue which are designated as the *optic lobes,* and back of these, the *medulla oblongata* and *spinal cord.* The optic lobes are highly developed in these animals. They aid in controlling motor actions, and correspond, therefore, to the corpora quadrigemina of the mammals. In the higher animals these bodies are not very conspicuous, because their function has been transferred in a large measure to other parts of the nervous system.

The Complex Brain.—The functional development of the brain requires an increase not only in its size and weight but also in its complexity. Having reached the group of the mammals, the first factor becomes of lesser importance than the second, because it is readily noted that the brains of neighboring species then frequently possess practically the same weight, although their functional capacity is decidedly different. Any additional mental power is finally gained by rendering the brain more uneven. Numerous furrows or *sulci* are developed in its outer zone which subdivide its external surface into numerous long and narrow *convolutions,* usually pursuing a course from before backward. The weight of the cerebrum amounts to 1500 grams in the human male and to 1350 grams in the human female. Its weight increases rapidly up to about the fifth year, but remains practically stationary after the eighteenth year. Only the whale and elephant have a heavier brain than man, although the intelligence of these animals by no means equals that of man.

This increased complexity of the higher brain signifies that it gives lodgment to a much larger number of neurones than the lower, these elements being required for the psychic processes of reflection, intelligence, and volition. Thus, the human brain has lost much of that kind of nervous material which accomplishes the ordinary reflex interchanges. Instead, it has acquired a certain number of nervous units

in which those associations arise that impart a distinct psychic quality to their more fundamental processes.

As has been stated above, this additional number of neurones finds sufficient space in the brain by virtue of the folded condition of its surface, every additional furrow serving as a depository for these cells. This arrangement calls to our minds the manner in which the area of the alveolar surface of the lungs is increased to augment diffusion. To

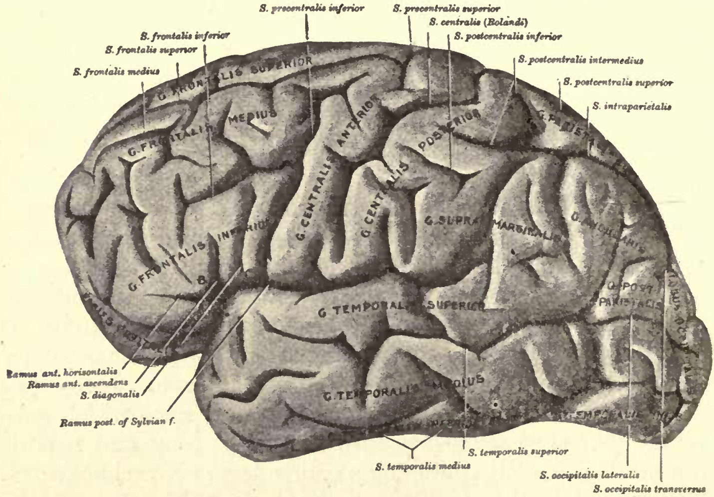


FIG. 121.—Left cerebral hemisphere from the lateral aspect. (*J. Symington.*)

begin with, these organs appear in the form of two separate pouches, possessing perfectly smooth inner surfaces. When, however, the constantly increasing metabolic requirements of these animals necessitate a more ample interchange of the gases, the formerly single air spaces are subdivided into many by thin partitions projecting inward from their walls. These partitions become confluent in the higher forms, so that each lung is subdivided into many millions of minute air-cells or alveoli.

The Arrangement and Structure of the Gray and White Matter.—Contrary to the spinal cord, the gray matter of the

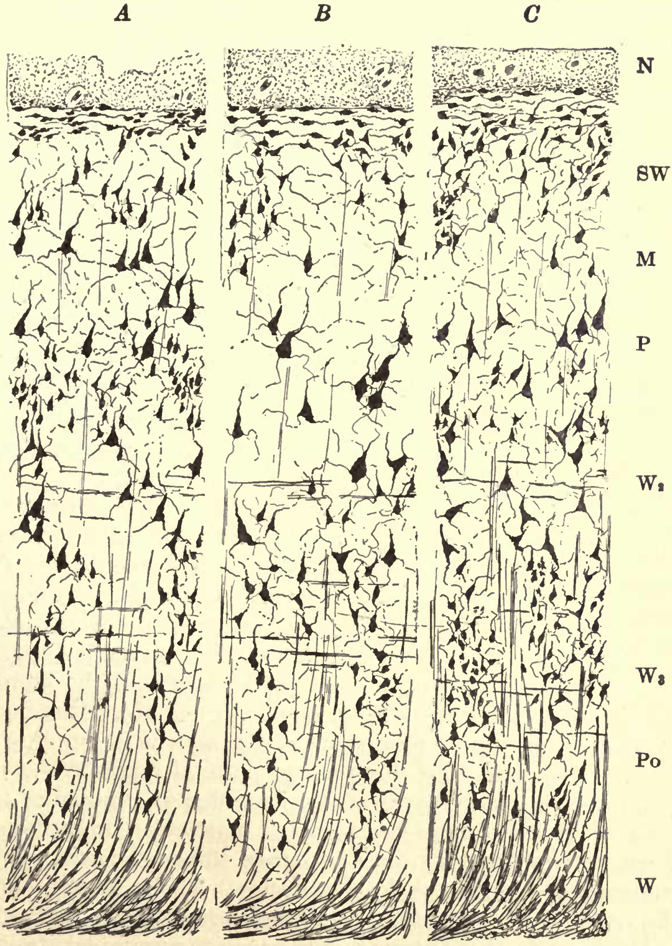


FIG. 122.—Cross-section of *A*, cortex of frontal convolution; *B*, cortex of posterior central convolution; *C*, cortex of middle occipital convolution. *N*, neuroglia; *SW*, superficial white fibers; *M*, molecular layer; *P*, pyramidal cells; W_2, second transverse fibers; W_3, third transverse fibers; *Po*, polygonal cells; *W*, white matter.

brain is situated outside the white matter. Thus, any cross-section of the cerebrum or cerebellum invariably presents an outer zone of a grayish-red substance situated next to the pia mater, and an inner core of white matter. This arrangement leads us to suspect that the cell-bodies of the various neurones lie directly below the surface of the brain, while the fibers forming their afferent and efferent connections occupy a position centrally to them.

If a histological preparation of the cerebrum is placed under the high power of a microscope, it will be seen that its cortical substance consists of a supporting framework of neuroglia tissue, in which are embedded the cell-bodies and central processes of a large number of neurones. These cell-bodies are arranged in several layers and possess in most instances a pyramidal shape. Their tips are directed outward, while their broad basal portions are turned inward and send a well defined axone into the underlying white matter.

A general idea regarding the minute structure of the cerebral cortex may be obtained from Fig. 122. As has been emphasized above, its most conspicuous elements are the pyramidal cells of the motor realm. It should be remembered, however, that this histological picture changes considerably in the different regions of this organ. Thus, it should be noted first of all that the thickness of the human cerebrum varies from 4 mm. to 2 mm., and furthermore, while its posterior realm is characterized by a prominent layer of granular cells, its upper or parietal region embraces a zone of very large pyramidal cells which are known as the cells of Betz. These cells are of particular importance, because they generate those impulses which give rise to the contractions of the skeletal muscles. Their axones enter the cerebral white matter, and finally descend in the spinal cord through the anterior and crossed pyramidal tracts, two typical efferent paths of the projection-system. It will be shown later that all these fibers cross to the opposite side, this crossing being effected either in the medulla oblongata or in the spinal cord itself.

CHAPTER XXXIII

THE CEREBRUM

The Different Regions of the Cerebral Cortex.—The cerebrum is composed of two halves or *hemispheres* which are separated from one another by a deep furrow, termed the *great longitudinal fissure.* The floor of this cleft is formed by a narrow bridge of white matter connecting the two hemispheres with one another. It is designated as the *corpus callosum.* From the little brain or *cerebellum,* the cerebrum is separated by a deep horizontal depression which gives lodgment to a strong septum of dura mater, the *tentorium cerebelli.* The outer convex surfaces of the cerebral hemispheres, as well as their flat median surfaces adjoining the longitudinal fissure, present numerous grooves or sulci which subdivide these areas into many smaller ones, possessing as a rule a long and narrow shape. Two of these fissures are very clearly outlined, their conspicuousness enabling us to employ them as general landmarks in localizing the functions of this organ. They are known as the *fissure of Rolando* and *fissure of Sylvius.* The former is situated about the middle of the outer surface of the hemisphere, and pursues an oblique course forward and downward from the longitudinal fissure, beginning about half an inch behind the mid-point between the globella and the occipital protuberance. The latter begins at the base of the brain at a distance of about 5 cm. behind the external angular process, and runs outward to the external surface of the hemisphere.

These fissures, together with the parieto-occipital groove, divide the external surface of each cerebral hemisphere into five lobes: namely, the frontal, parietal, occipital, temporo-sphenoidal, and island of Reil. The *frontal lobe* is situated in front of the fissure of Rolando and above the fissure of Sylvius. Back of the fissure of Rolando lies the *parietal*

lobe, its posterior boundary being formed by the parieto-occipital fissure, and its lower boundary by the horizontal limb of the fissure of Sylvius. The posterior pole of each hemisphere is formed by the *occipital lobe.* Below the fissure of Sylvius lies the *temporal lobe,* which occupies practically the entire middle fossa of the skull. The *island of Reil* is hidden from the view, because it is situated in the fissure of Sylvius at the base of the brain.

The most important fissure upon the inner or median surface of the cerebral hemisphere is the calloso-marginal. It pursues a course upward and backward, parallel to the corpus callosum. The calcarine fissure is of importance to us at this time, because it indicates the location of the center of sight. This groove eventually joins the parieto-occipital fissure.

The fibers emerging from these cortical areas of gray substance, make three principal connections: namely, (*a*) with other areas of the same hemisphere; (*b*) with areas in the opposite hemisphère; and (*c*) with the spinal cord and distant parts. The first form the so-called *association system,* the second, the *commissural system,* and the third, the *projection system.* Notice should also be taken at this time of the fact that two important masses of gray matter are situated below the cortex and directly in the path of the projection fibers. They are the *optic thalami* and the *striate bodies.* The former lie one to each side of the third ventricle and below the lateral ventricle, thus forming a deposit of gray matter upon the upper surface of each *crus cerebri.* The crus, as has been stated above, represents the most compact portion of the bundle of fibers passing away frcm the cerebral cortex and striving to attain the narrow point of exit afforded them in reaching the medulla. The striate bodies are situated somewhat in front of the optic thalami, and form a prominence upon the floor and wall of the lateral ventricle. Each striate body, however, embraces two parts, one lying directly in front of the thalamus in the position just indicated, and one at the side of this mass of gray substance.

The Removal of the Cerebrum.—In analyzing the functions of the different segments of the central nervous system,

use is generally made of several different methods which may be grouped under the following headings: (*a*) removal or enucleation of the part under observation; (*b*) stimulation of its cortical gray matter or underlying white matter; (*c*) tracing of the fibers connecting it with other structures, and (*d*) observation of the symptoms accompanying inflammatory and destructive lesions of its substance. Of particular importance is the study of clinical cases, because it permits us to substantiate the conclusions drawn from the results of experimental lesions in animals. Thus, while it is a comparatively simple matter to note losses of motor function in animals, it is usually impossible to detect disturbances of the sensations, because in the latter case we are almost wholly dependent upon the description of sensory impressions, which an animal cannot give. For this reason, the physiologist must gain his information in most instances from an analysis of the disturbances following certain pathological lesions of the nervous system of man. Such lesions are by no means uncommon and usually result in consequence of hemorrhages, injuries, and the growth of tumors.

Let us see first of all what changes are evoked by the removal of the cerebral hemispheres. Attention has already been called in Chapter XXII to the fact that this procedure destroys the psychic life of the animal, whether simple or complex. Accordingly, it may be surmised that this structure is the seat of associative memory. This brief statement may be greatly amplified by studying the behavior of any one of those animals whose general movements remain practically the same after the loss of this part of the nervous system. Thus, it may be gathered from the behavior of the shark after the removal of its cerebrum that the fish are only slightly affected by the loss of this structure. They reveal the same power of movement as normal animals, although invariably tending to assume a rather continuous position of rest which is exchanged for one of activity only upon stimulation. But when made to move, their motor reactions exhibit a perfectly normal character.

Very similar changes are presented by the decerebrated frog. Its usual attitude is one of inactivity, although it

maintains its posture so well that it cannot easily be detected when allowed to mingle with a number of other perfectly normal frogs. One way of establishing its identity is to pass the hand over the aquarium. The normal frogs will then make muscular efforts to escape, because although not able to form distinct visual concepts, such a movement is received by them as a "shadow" possessing, possibly, certain injurious consequences. Since the actions of the decerebrated frog are no longer controlled by associations, it retains its position even in the direct path of danger.

Very similar conclusions may be drawn from the changes taking place in the "act of croaking" after the cerebrum has been removed. Ordinarily, the frog produces its characteristic sounds only when the conditions in the pond are perfect. Subsequent to the loss of the cerebrum, however, this formerly associative act assumes the character of a simple reflex. Thus, it may now be elicited at any time by simple stimulation, such as may be produced by touching the back or sides of the frog. In the absence of the cerebrum these tactile impacts evoke a contraction of the resonating pouches without being first acted upon by the higher centers. Volition has been definitely removed from this reaction.

A frog deprived of its cerebrum jumps and swims normally and rights itself when placed upon its back. Its balancing movements reveal a perfectly normal character. It reacts to stimuli applied to its nasal mucosa, and avoids obstacles. Furthermore, its digestive processes are not impaired, although it will not eat spontaneously. But since its simple as well as automatic reflex mechanisms are in perfect condition, an animal of this kind may be kept alive for many years provided it is placed in proper surroundings and is fed from time to time. If the food is placed in its mouth, it is swallowed and digested in a normal manner.

Practically the same behavior is manifested by birds after they have been deprived of their cerebral hemispheres. Thus, the decerebrated pigeon continues in an inactive state for long periods of time, but may be made to move at any time by stimulation. If tossed into the air, it will fly, but not for any length of time. Moreover, in alighting it will

select practically any perch and even one that may prove injurious to it. As has been stated above, the removal of the cerebrum destroys associative memory. In consequence of this loss the animal is no longer able to profit by experience. Thus, the decerebrated pigeon will not take food even when placed directly in front of it, but if fed and taken proper care of, it will live practically as long as a normal one. Its life, however, is that of a simple reflex animal.

Very similar results have been obtained in cats, dogs, and monkeys. In these animals, however, the removal of the cerebrum is a much more difficult task than in the lower forms, because their cerebral white matter embraces a number of subcortical and basal masses of gray matter, the destruction of which gives rise to certain motor disturbances of a general character. For this reason, the enucleation of the cerebrum in mammals should be restricted to its cortical portion and adjoining white matter. It may suffice to refer at this time to three decerebrate dogs, the behavior of which was carefully studied for as long a time as eighteen months after the operation. These animals began to move about within a few days after the operation and even walked across inclined planes. They avoided obstacles and reacted to diverse sensory stimuli by snarling, barking, and the erection of the ears. Their motor reactions, however, were not controlled by associations. The greatest part of each day was spent by them in absolute rest. They did not seek food, but finally took it when it was placed directly in front of them.

The aforesaid general deductions pertaining to the function of the cerebrum are also applicable to man. We are reminded at this time of the disturbances accompanying general paresis (softening of the brain) which condition most closely resembles that established in the lower animals by the experimental removal of the cerebrum. The power to acquire new memory reactions is lost and even the stored memory concepts gradually pass out of existence, until the formerly intelligent behavior of the person closely approaches that of a reflex animal.

Nature also supplies us constantly with many very instruc-

tive, although deplorable, cases of partial destruction of the central nervous system. We are reminded at this time of the lacerations of the cerebrum by bullets and other solid bodies as well as of the destruction of certain areas of this organ by hemorrhages, tumors, and inflammations. The case most frequently cited in the literature is that of a stone-cutter who permitted an iron rod to slip into a borehole, into which he had previously placed a certain amount of dynamite. The rod traversed his skull from below upward, tearing away a very considerable portion of his frontal lobes. Curiously enough, this severe injury was followed by an uneventful recovery. Nothing more than a relatively slight retrogressive change in his character and intelligence could be noted subsequent to the injury.

Many cases of inherited absence of the cerebrum have also been recorded. These infants showed a persistence of the spinal reflexes, and particularly those of mastication, sucking, crying, and grasping. Of particular interest is the case of a child whose cerebrum was destroyed by disease when about two years of age. Two years later it was found at autopsy that the cranial cavity was filled with fluid (hydrocephalus). During the interim the child lay passive in its bed as though sleeping, giving no signs of intelligence or initiative purposeful movements. Its spinal and bulbar reflexes, however, were well preserved.

CHAPTER XXXIV

THE LOCALIZATION OF FUNCTION IN THE CEREBRUM

The Motor Area.—The cerebral hemispheres have been regarded as the material seat of consciousness since antiquity. Thus, it was believed that their frontal regions subserve imaginative qualities, while their central portions give rise to intelligence, and their posterior realms to memory. This localization of the psychic processes in different regions of the cerebrum has been made thorough use of by the originators of the "science" of phrenology. It was proposed by them that the character, behavior and accomplishments of men can be correlated with the contours of the brain, and that the varying development of the different segments of the latter evokes corresponding changes in the general configuration of the skull. Thus, it was conjectured that a musician must present an excessive development of the temporal lobes and an unusual prominence of the corresponding regions of the cranium. For similar reasons, a person skilled in sketching and painting was supposed to develop in time an extraordinary prominence of the occipital areas of the cranium.

While in the light of our present-day knowledge a moderated conception of this kind can be successfully defended, the phrenologists were not satisfied with simple statements, but extended their localization practically to all human traits and endeavors. In accordance with their chiefly hypothetical doctrines the skull is beset with an almost unlimited number of "bumps" which are employed by them to analyze the present and future qualities and possibilities of the person. Accordingly, this conception was exploited in a commercial way by advising the person what calling in life he should follow in order to make the best use of his cerebral peculiarities. These often far-fetched inferences derived

from imaginary details of the outline of the cranium, gradually brought phrenology into lasting disrepute

Opposed to this view embodying the principle that the cerebrum is a plurality of organs, is the one which holds that this organ is absolutely homogeneous in its structure and function, and gives rise to consciousness in the form of an indivisible product. During the years of 1825 to 1850, however, Broca and others collected certain evidence which

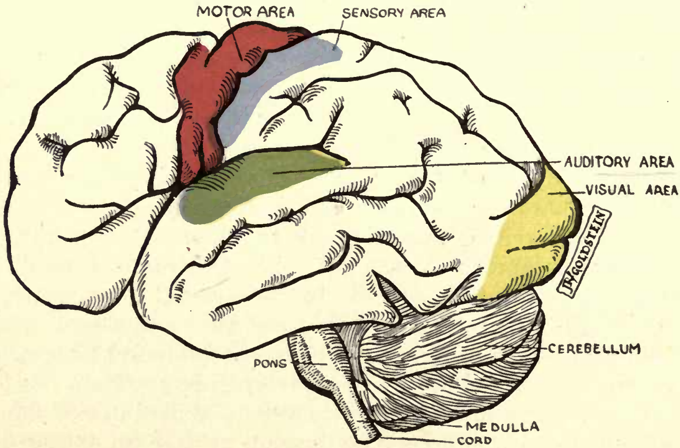


Fig. 123.—Cerebral localization (external surface).

showed that speech is controlled by a circumscribed area situated in the front part of the left cerebral hemisphere. Somewhat later Jackson proved that the muscular spasms characterising epilepsy result in consequence of an excitation of the cerebral cortex. Then followed the observations of Fritsch and Hitzig, which demonstrated that the surface of the cerebral cortex is irritable. These investigators demonstrated that the electrical excitation of a definite realm of the cerebrum gives rise to contractions of certain skeletal muscles. For this reason, the term *motor area* has been applied to this circumscribed region of the cortex.

In the cat, dog, and monkey the motor area occupies the region in front and behind the fissure of Rolando, while in the apes and man it embraces solely the anterior central convolution of each side. If either area is now more carefully mapped out, it will be found that the cellular constituents of its upper portion situated next to the horizontal fissure, govern *the muscular reactions of the trunk and legs.* At a somewhat lower level are found those ganglion cells which innervate the *muscles of the arms*, and at a level opposite the lower end of the aforesaid fissure, those cells which control the *movements of the face.* Thus, it may be stated that the motor field of the cerebral cortex is divided into a right and a left area, and each area in turn into three minor realms. In fact, by employing a special set of electrodes, it is possible to evoke even more minute movements, such as flexion and extension of the fore- and hind-limbs, as well as movements of the muscles of the tongue and eyes.

It will be remembered that these areas contain large, pyramidal ganglion cells which are known as the cells of Betz. It has already been stated above that the axones emerging from their cell-bodies, traverse the cerebral white matter and enter the spinal cord, where they form synapses with efferent neurones of the second order. It is to be noted, however, that all these fibers eventually gain the opposite side of the cord either by crossing in large numbers in the medulla oblongata or more gradually as they descend through the spinal efferent tracts. The fibers effecting their crossing in the medulla, form a very conscript path to which the name of *pyramidal decussation* has been given. This decussation of the efferent fibers of the projection system lies in relation with a similar crossing of the sensory fibers of the same system.

The fact that the nerve cells of the motor areas control the actions of the muscles on the opposite side of the body, should make it evident to us that an injury to either one of them must result in a paralysis involving the opposite musculature, excepting the muscles of respiration. This condition which is known as *hemiplegia,* is brought about at times by a stroke upon the fronto-parietal region of

the cranium and consequent escape of blood from one of the dural vessels into the neighboring cerebral cortex. The blood may also accumulate upon or below the dura mater and exert a direct pressure upon the underlying motor area.

In this connection brief reference should also be made to that form of *epilepsy* which finds its origin in a mechanical excitation of the cerebral cortex. It is common knowledge that persons afflicted with this disease, suffer from periodic attacks of violent muscular spasms, each attack being initiated by tremors and twitchings of a particular muscle or groups of muscles. The neighboring muscles are involved gradually until the body as a whole is retained in an almost continuous state of spasmodic contraction. These seizures last for varying periods of time, and are repeated as a rule at irregular intervals. In many instances, these attacks are the direct result of cerebral excitation. A projecting piece of bone, the remnant of an earlier fracture of the cranium, may press upon the motor area, or an extravasation of blood may have taken place in consequence of an injury to the head which gives rise to a mechanical irritation of the neighboring gray matter. If traceable to a local cause of this kind, the epileptic seizures will cease after the exciting agent has been removed by operation.

The Body-sense Area.—The impulses from the cutaneous sense-organs are relayed to that portion of the cerebral cortex which is situated directly behind the fissure of Rolando. Besides the posterior central convolution, this area also embraces the anterior portion of the parietal lobe. This localization is based chiefly upon histological data, because the sensory fibers ascending through the spinal cord, form a median bundle which terminates in the gray matter at the base of the brain, whence tertiary fibers conduct these impulses to the parietal cortex. Further evidence of this character has been derived from the direct stimulation of the surface of the parietal lobes in conscious patients, this procedure having been employed in these instances for diagnostic purposes. These patients perceived sensations of touch and numbness as long as the stimulation remained confined to this particular area of the cerebrum.

Some doubt exists as yet regarding the character of the sensations mediated by this area. Since pain is not felt as a result of the excitation of this cortical field, it is commonly believed that the associations formed here pertain solely to touch, temperature, and muscular sensibility. Obviously, if these sensations are intended to give rise to motor reactions, they are relayed from this area to the neighboring

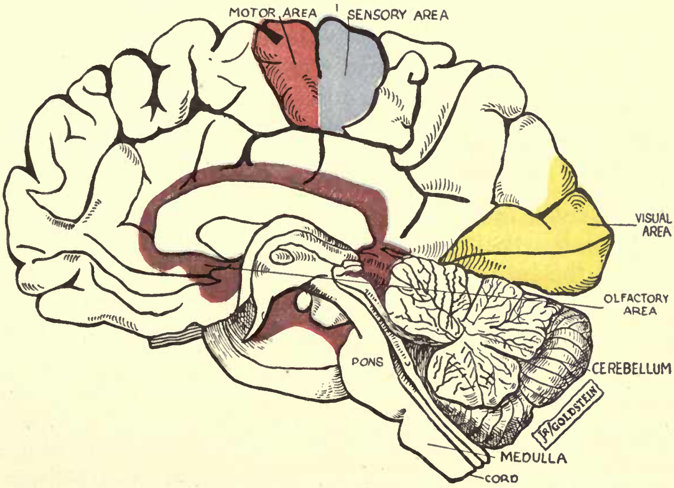


Fig. 124.—Cerebral localization (median surface).

motor realm, and by way of the corpus callosum to the corresponding area in the opposite half of the cerebrum.

The Center for Sight.—The changes noted after the destruction of the occipital lobes, either experimentally or by pathological processes, have proved conclusively that the impulses derived from the retinæ are associated in this particular region of the hemispheres. The area most directly concerned is the one situated along the calcarine fissure on the mesial surface of each hemisphere. In many animals the fibers emerging from the eyes cross over in their entirety to the center on the opposite side. Accordingly, the destruction of one occipital lobe would cause a blindness in the opposite

eye. In man, however, the crossing is incomplete, because the fibers from the outer halves of the retinæ always remain on the same side, whereas those from their inner halves seek the opposite center. Thus, it will be seen that the ablation of, say, the right occipital cortex must destroy the sight in the outer half of the right eye and inner half of the left eye.

This is the condition of *half-blindness* or *hemianopia*. The yellow spot of each retina which is its most sensitive area, is not involved in this blindness, because the fibers emerging from it find representation in both occipital centers. It will also be seen that the loss of the receptive power of, say, the right halves of the retinæ must blot out the left fields of vision, because the objects situated to the left of the visual line of the eye, are always focalized upon the right side of its retina.

The Center for Hearing.—By similar means it has been demonstrated that the impulses derived from the organ of Corti of the internal ear, which forms the receptor for the sound waves, are relayed through the eighth cranial nerve and various parts of the brain-stem until they arrive in the cortex of the temporal lobe. The area most directly involved is the upper convolution of this lobe, while the middle and inferior ones are set aside for memory concepts pertaining to sounds. The auditory fibers also cross in large numbers to the opposite center, so that the destruction of either temporal lobe cannot produce permanent deafness, because the function of this area is then taken up by the one on the opposite side.

The Centers for Smell and Taste.—It is a well known fact that the sense of smell is very unequally developed, because some animals, such as the dolphin and porpoise, are entirely deficient in olfactory organs, while others, such as the dog, rat, and opossum, show a high development of this sense. These sensory impulses ascend from the olfactory area in the nasal cavity through the olfactory nerve into the anterior realm of the cerebrum. They are finally relayed to the distal limb of the hippocampus, where they find psychic representation. The sensations of taste are conveyed to the cerebrum by the fifth, ninth, and tenth cranial nerves. They are

associated in the hippocampal area near the anterior end of the temporal lobe.

The Centers for Speech and Writing—At birth, the cerebrum is practically a potential organ as far as its higher functions are concerned, while later in life it serves as a register of memory concepts, controlling the diverse activities of the body. Possibly the most remarkable acquired faculty is the production of coherent sounds in the form of speech. While practically all the higher animals possess the power of uttering purposeful sounds, none is able to produce them in such an articulated manner as man. We speak in consequence of associations derived from various sensory impressions. Thus, the centers for sight, hearing, taste, smell and touch may be said to be contributory to speech. The concepts formed with the aid of these centers, are again analyzed by a group of ganglion cells which are usually said to be situated in the left inferior frontal convolution. This rather definite localization of the speech center, however, leaves out of consideration the fact that speech is a combined faculty and cannot really be restricted to this narrow sphere. Thus, while it has been stated by Broca that the destruction of the left inferior frontal convolution leads to a *loss of speech* or *aphasia*, it has been shown in more recent years that this result may also follow lesions in other parts of the cerebrum, chiefly its association areas for sight and hearing.

It may, therefore, be stated in a very general way that speech is made possible by an effector, the larynx, the different parts of which are under the control of certain ganglion cells situated in the motor area of the cerebrum. These cells, together with the corresponding efferent fibers of the vagus nerve, constitute the efferent or motor circuit of the speech mechanism. Furthermore, the impulses discharged by these cells are regulated by a special group of ganglion cells forming the speech center proper. The activity of the latter is in turn controlled by others of the same character, constituting the association realms for sight, hearing, etc. Because of these close connections, a loss of speech or aphasia must follow injuries to the center as well as to any one of its contributary association realms. The term aphasia, how-

ever, signifies that the lesion is situated within the cerebrum. Consequently, a loss of speech resulting from an injury to the larynx or its efferent paths, cannot rightly be called aphasia.

Practically the same statements may be made regarding the nervous mechanism controlling the act of writing. The location of its efferent or motor channel need not be considered in detail. It embraces those cells and fibers of the motor area which control the muscular actions of the arms and hands. As in the case of speech, the activation of this mechanism is dependent upon diverse afferent impulses and their proper association. Consequently, the act of writing is a combined faculty and cannot be sharply localized, although sufficient clinical evidence is at hand to show that its chief center lies in the frontal lobe in close proximity to the psychic area for speech.

CHAPTER XXXV

THE CEREBELLUM AND MEDULLA OBLONGATA

The Structure of the Cerebellum.—The cerebellum is situated directly below the posterior lobes of the cerebrum, but is separated from the latter by a dense septum of dura mater, called the tentorium. It occupies the posterior fossa of the base of the cranium, and measures close to four inches from side to side, about two and one-half inches from before backward, and two inches in thickness near its center. Its average weight is 140 grams or about one-tenth of the weight of the entire brain. In infants, however, its size is proportionately much smaller than in adults. Like the cerebrum it consists of two halves or *hemispheres* which are connected with one another by a median portion, *the vermis.* The latter appears to be the fundamental part of this organ, because in the lower forms, such as the fishes and reptiles, the hemispheres attain only a very rudimentary size. The surface of this structure is not convoluted, as is that of the cerebrum, but is folded by numerous transverse furrows into lamellæ-like strips, bearing a close resemblance to the sprigs of the cedar tree.

If a cross-section of one of these lamellæ is placed under the ocular of a microscope, it will be seen to be composed of an outer zone of gray matter and an inner zone of white matter. The gray matter consists of three layers. The innermost, lying in relation with the white matter, is known as the *nuclear layer,* and the outermost, as the *molecular.* Between these two zones is placed a row of very large cells each of which possesses a pear-shaped cell-body and bushy, fan-shaped dendrites. These very characteristic elements of the cerebellar cortex are designated as the *cells of Purkinje.* Their axones traverse the white matter and form connections with the central nuclei of gray matter, situated within the vermis.

The cerebellum is the dorsal outgrowth of the brain-stem, and lies really outside the main paths connecting the cerebrum and spinal cord. It is, however, closely related to the aforesaid parts by bridges of fibers, forming the *superior, middle and inferior peduncles*. Possibly the most striking structural peculiarity of the cerebellum is the uniform arrangement of its elements. In the cerebral cortex, on the other hand, we have noted certain differences in the shape

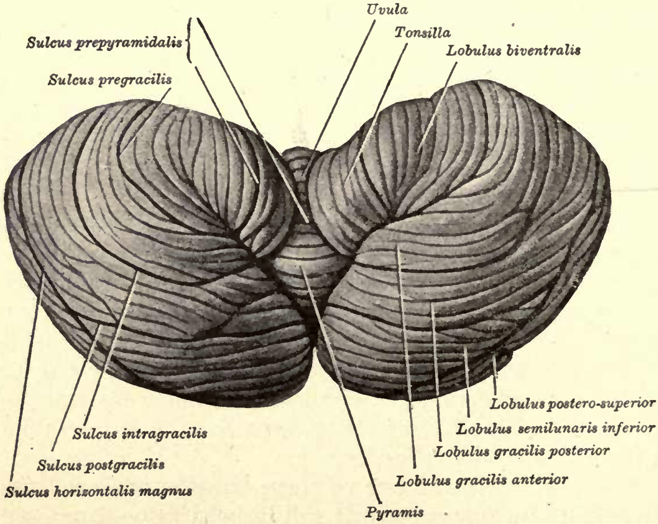


FIG. 125.—View of cerebellum from below. (*J. Symington.*)

and size of its constituent cells as well as in their position and general arrangement. In agreement with its structural diversity, we have observed that this organ consists of several parts contributing singly to consciousness. Accordingly, the fact that the gray matter of the cerebellum presents everywhere the same structural details, may rightly prompt us to conclude that its function is homogeneous in character.

The Function of the Cerebellum.—Even a very casual comparative study of the cerebellum will show that its size and complexity vary greatly in different animals. Although

of large size in man and the apes, it is not so preponderant as in the birds and fishes. This fact leads us to suspect that it is not related to intelligence, but rather to the locomotor powers of the animal. In brief, it appears to subserve the co-ordination of muscular movements, and particularly those concerned in locomotion. Ordinarily, the body is in a condition of *synergia*, which implies that its movements are executed with purpose, force, steadiness, and coherence. Contrariwise, an extensive laceration of the cerebellum invariably induces a condition of *asynergia* or loss of the power properly to co-ordinate muscular movements. This change originates in a loss of the tonus and force of the skeletal muscles, and an unsteadiness and incoherence in their actions.

This view, attributing to the cerebellum the function of an organ of muscular co-ordination, is based in a large measure upon the symptoms following the destruction of this organ in certain animals. A number of clinical cases, however, have also been recorded which show that the conclusions drawn from these experiments on animals are in the main applicable to man. Inasmuch as the birds are very closely dependent upon a properly balanced muscular apparatus, it cannot surprise us to find that they are most profoundly affected by the loss of this organ. Thus, a decerebellate pigeon cannot fly and cannot even keep on its feet. It loses its balance with every move, and may, in fact, injure itself if not carefully protected. It is to be noted especially that this loss of the power of co-ordinated movement is not due to a paralytic condition of the skeletal muscles, but to an inability on the part of the pigeon to correlate the contractions of these organs.

Very similar symptoms are displayed by the decerebellate dog. It is true, however, that a certain adjustment sets in later on, and that the aforesaid functional disturbances assume a milder character as the months pass by. Any forced movement, however, causes them to reappear in all their former intensity. Ordinarily, any swaying of the body is quickly compensated for by an appropriate counter-movement. This power is regained to a certain extent by the

decerebellate animals, although a certain awkwardness, unsteadiness, and susceptibility to fatigue remain behind as permanent results of this lesion.

By virtue of its power to co-ordinate muscular movements, the cerebellum has always been regarded as an important factor in the preservation of the equilibrium. But this function cannot be attributed exclusively to this organ, because the sense of orientation is really dependent upon a number of impressions derived from such receptors as the semicircular canals, the retinæ, the tactile corpuscles of the skin, and the muscle-spindles. All these sense-organs unite in contributing impulses which are relayed to central parts and eventually influence the musculature through the agency of the cerebellum, so as to obtain co-ordinated and purposeful muscular responses. Accordingly, it cannot justly be stated that this organ is the "center" for equilibration. It is merely a link in the chain of structures mediating this function.

It is true, however, that the combined action of these receptors is easily offset. This fact may be readily demonstrated by standing close to the edge of a precipice. Under ordinary circumstances we make use of objects near at hand in judging our position in space, and hence, when suddenly brought into relation with objects which are hundreds of feet away from us, our usual mode of interpreting spacial relationships no longer suffices to give us our bearings. Vertigo, muscular tremors, and other dangerous symptoms then develop, which are easily explained physiologically. These symptoms may gradually be mitigated by experience or may be more quickly remedied by glancing at familiar objects at the side or back of us.

The importance of the eyes in orienting ourselves increases as the acuity of the other receptors diminishes. This point may well be illustrated by a brief consideration of the behavior of those persons whose muscle-sense has been partially destroyed. It is a familiar fact that the disease of locomotor ataxia is characterized by a degeneration of the posterior roots of the spinal cord. A person so afflicted cannot stand erect with the eyes closed, because those

afferent paths which convey the sensations from the muscles, have been partially destroyed by this degeneration. He reels and falls almost as soon as his feet are brought together for the purpose of testing his power of equilibration.

The *muscle-sense* finds its origin in impulses which are produced in the sensory terminals of the skeletal muscles in consequence of the contraction of their constituent fibers. It is a well known fact that we may close our eyes and still be able to tell the position in space of any one of our parts. It appears that these concepts are the result of certain impulses which arise in consequence of the varying degrees of pressure brought to bear by the contracting muscle fibers upon the aforesaid nerve filaments. Other important contributing factors to equilibration are the *static and dynamic senses* which are mediated through the agency of the utricle and semicircular canals of the internal ear. The structure and function of these receptors will be more fully discussed in a subsequent chapter.

The Medulla Oblongata or Bulb.—The medulla forms the upper enlarged portion of the spinal cord and appears, therefore, as a part of this structure. In conformity with its close anatomical relationship to the latter, it may be said to be an organ of *conduction* as well as one of *reflex and automatic action.* It occupies a position directly in the path of the cerebro-spinal fibers, and besides, forms an important relay-station upon the tracts of the cranial nerves. The centers contained in it are of two kinds: namely, simple, reflex and automatic. Because of the fact that it embraces the nuclei of several cranial nerves, it becomes the central controlling agent of a number of simple reflex acts, such as are concerned with the closure of the eyelids, mastication, deglutition, vomiting, sneezing, and coughing.

In addition, the medulla embraces three very important automatic centers: namely, that regulating the activity of the heart, that controlling the functions of the respiratory organs, and that determining the caliber of the bloodvessels. It has already been mentioned that the *cardiac center* is connected with the heart by means of the vagus nerves and possibly also by means of definite sympathetic fibers. The

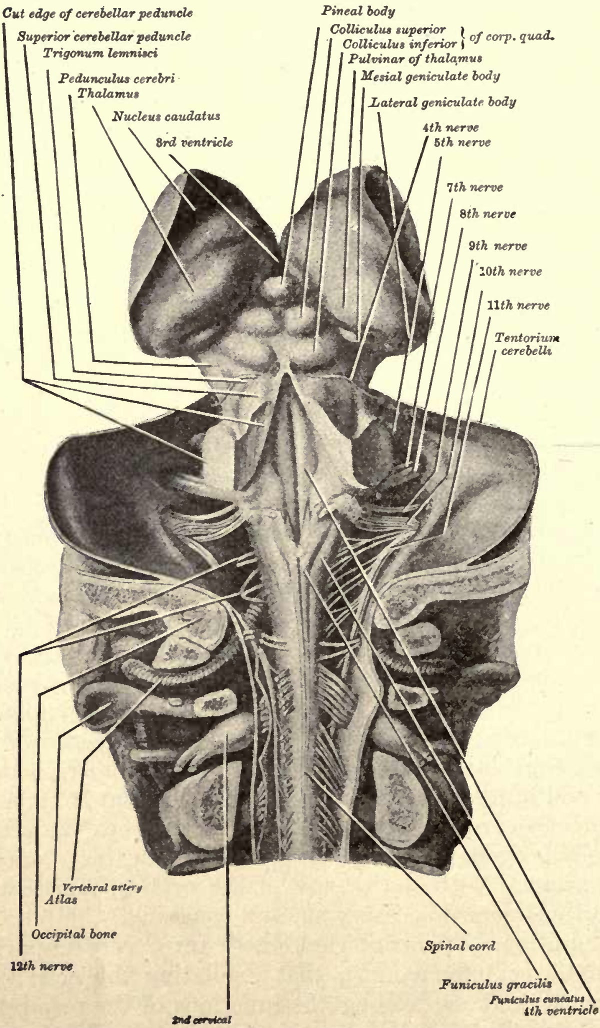


FIG. 126.—View of dorsal aspect of upper part of the spinal cord, medulla oblongata, pons, fourth ventricle, mid-brain, thalamus, etc., dissected *in situ*. (*J. Symington.*)

destruction of the medulla, however, does not necessarily stop the function of this organ, because it is automatically active. It then merely loses those controlling influences which correlate its activity with those of other organs. The *respiratory center* is normally stimulated by the carbon dioxid of the blood, although it may also be influenced by diverse afferent impulses. Inasmuch as it controls the action of the muscles of respiration, its destruction must lead to an almost immediate standstill of the respiratory mechanism, and hence, terminate life within a very short time. The *vasomotor center* regulates the size of the blood-bed. Its destruction leads to a relaxation of the bloodvessels, and fall in bloodpressure.

The Cranial Nerves.—The medulla oblongata and parts above it give off twelve pairs of nerves to each side of the head, which form an interlocking system regulating several independent functions. The last six of these arise from the medulla itself. Their course and function may be briefly summarized as follows:

1. The *olfactory nerve*, or nerve of smell, arises in the sensory nerve cells of the olfactory area of the nasal cavity. Its fibers traverse the pores in the cribriform plate of the ethmoid bone, and by relays attain the olfactory bulb. The center of smell is situated in the hippocampal region. Connection is formed with the latter by three paths which are known as the medial, intermediate and lateral olfactory striæ.

2. The *optic nerve*, or nerve of sight, conveys the impulses from the retinæ to the thalami, whence they are transferred to the visual center in the occipital lobes of the cerebrum. In man these fibers effect a partial crossing in the optic chiasma. As has been stated above, this crossing permits those fibers which are derived from the inner halves of the retinæ, to reach the opposite half of the cerebrum. The outer fibers remain on the same side.

3. The *oculomotor nerve* arises from a nucleus situated in the central gray matter near the floor of aqueduct of Sylvius. This nerve is motor in its function and innervates the internal, superior and inferior recti muscles as well as the inferior oblique muscle of the eyeball. In addition, it controls the sphincter muscle of the iris, as well as the ciliary muscle.

4. The *trochlear nerve* arises from a nucleus situated close to that of the oculomotor nerve. It is a motor nerve, supplying fibers to the superior oblique muscle of the eyeball.

5. The *trigeminal nerve* has two roots, one motor and the other sensory. Near the apex of the petrous portion of the

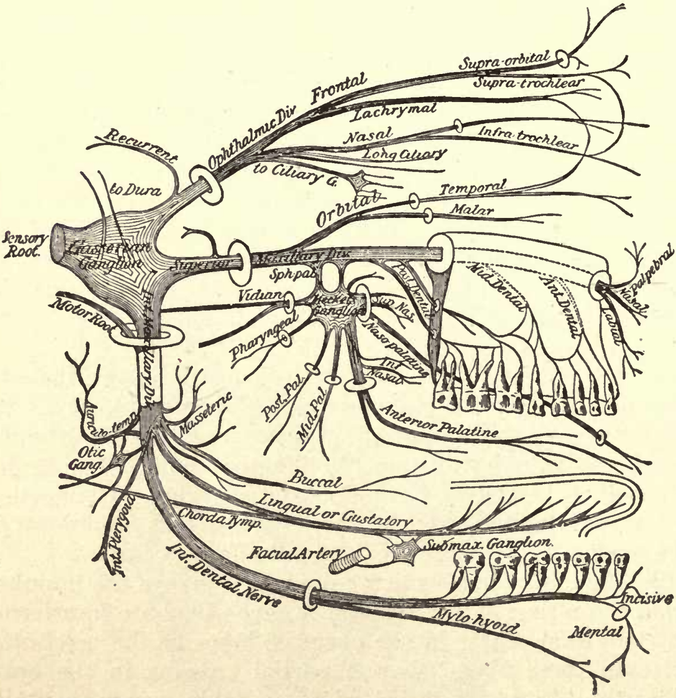


FIG. 127.—Trigeminus nerve (From Potter, "Compend of Human Anatomy.")

temporal bone a large ganglion is formed which is known as the Gasserian or semilunar ganglion. Distally to this point the trigeminus is arranged in the form of three large branches which are termed the ophthalmic, superior maxillary and inferior maxillary nerves. Its *ophthalmic branch* is principally sensory in its function, and supplies the eyeball, lacrimal gland, mucous lining of the eye and nasal passage, as well

as the integument of the forehead, nose and region of the eyebrows. Its second division or *superior maxillary branch* is a sensory nerve. It proceeds forward from the Gasserian ganglion and terminates beneath the musc. lev. labii superiores into a number of branches which spread out upon the side of the nose, lower eyelid, and upper lip. Just before this nerve enters the orbit it gives off branches which pass through bony canals in the posterior surface of the superior maxillary bone and eventually reach the molar teeth. While traversing the infra-orbital foramen, this nerve also gives off branches which pass to the upper tricuspid, cuspid and incisor teeth.

The *inferior maxillary division* of the fifth cranial nerve traverses the foramen ovale. Its motor root joins the sensory division outside the cranium, both being situated in the zygomatic fossa. After their redivision, one branch is distributed to all the muscles of mastication excepting the buccinator. The other branch is chiefly sensory and divides into three minor ones: namely, the *auriculo-temporal*, to the tissues about the ear and the articulation between the mandible and temporal bones, the *lingual*, to the tongue, and the *inferior dental* to the lower teeth. These terminals are formed as this nerve traverses the mandibular canal in the body of the inferior maxillary bone. Just before entering this bony channel it sends some motor fibers to the mylohyoid and digastric muscles.

6. The *abducens nerve* is a motor nerve and innervates the external rectus muscle of the eyeball. Its nucleus lies below the colliculus facialis.

7. The *facial nerve* arises in the tegmental region of the pons, and is chiefly motor in its function. It is the nerve of expression, because it controls the muscles of the face, those of a part of the scalp, and those of the ears. Besides, it embraces secretomotor and vasomotor fibers for the submaxillary and sublingual glands which reach their destination by way of the chorda tympani. It also innervates the lacrimal glands.

8. The *auditory nerve* consists of two groups of fibers, namely, those concerned with hearing and those concerned

with the sense of equilibrium. The former pursue a circuitous course through the medulla, pons and lemniscus until they reach the psychic area for audition in the superior convolution of the temporal lobe. Those fibers which are derived from the semicircular canals, are relayed from the medulla into the central gray matter of the cerebellum.

9. The *glossopharyngeal nerve* is motor and sensory in its function. It arises from the side of the medulla, its motor fibers being distributed to the muscles of the pharynx and its secreto motor fibers to the parotid gland. Its sensory fibers convey impulses from the mucous membrane of the tongue, pharynx, tonsils, tympanic cavity, and eustachian tube.

10. The *vagus* or *pneumogastric nerve* emerges from the side of the medulla. It is a mixed nerve. The preceding discussions has shown that it is the principal nerve of respiration, because its branches innervate the larynx, trachea, and bronchi. It also conveys inhibitor fibers to the heart and sensory fibers from the arch of the aorta. It is the musculomotor nerve of the œsophagus, stomach and intestine, and sends secretomotor fibers to the stomach, intestine and pancreas.

11. The *accessory nerve* arises from the medulla and innervates the sterno-cleido-mastoid and trapezius muscles.

12. The *hypoglossal nerve* emerges from the medulla. It is a motor nerve and innervates the muscles of the tongue, inclusive of the geniohyoids and thyreohyoids.

The Autonomic Nervous System.—The name autonomic has been applied to that part of the nervous system which is self-active, although primarily controlled by the higher centers. Thus, we have seen that the heart, the stomach, intestine, urinary organs, and others may continue their functions even after they have been separated from central parts, although they cannot then be made to work in harmony with other structures. This system of nervous tissue possesses its own ganglia and simple reflex centers, as well as intricate networks of efferent and afferent paths. Its neurones, however, differ from those of the cerebro-spinal system in their structure as well as general arrangement. Thus, it is found that their cell-bodies are usually round,

while their axones are non-medullated throughout. Physiologically, they subserve non-volitional responses and are concerned with those reflexes which are evoked in the viscera. Among these might be mentioned the movements of the heart, œsophagus, stomach, intestine, ureter, bladder, and iris. In this group also belong the secretomotor, pilomotor and vasomotor reactions.

This visceral system of neurones is connected by several bridges with the cerebro-spinal system, so that an interchange of impulses may be effected at any time. It is to be noted, however, that this interchange takes place chiefly in an efferent direction, and that relatively few afferent impulses from the viscera actually reach consciousness. One of these connections is established with the help of several ganglia situated in the paths of the different cranial nerves, such as the fifth, seventh and tenth. It is usually designated as the *parasympathetic* division of the autonomic system.

Another very important bridge is formed at the level of the thoracic segment of the spinal cord. Certain ganglion cells which are located in the anterior gray matter of this portion of the cord, send out fibers which soon leave the anterior root and form connections with a number of ganglia situated along the vertebral column. This colony of ganglia and their ramification of fibers constitute the so-called *sympathetic* division of the autonomic system. In this way certain impulses of the cerebro-spinal system are enabled to enter the distant visceral system, because the aforesaid sympathetic ganglia are closely allied with the local nervous mechanisms in the different internal organs.

The sympathetic ganglia also embrace a certain number of neurones, the axones of which pass by way of special bridges into the cerebro-spinal system. These "recurrent" fibers intermingle with the other cerebro-spinal fibers and jointly form the mixed nerves of the spinal cord. By this means the different sympathetic impulses may also reach the smooth muscle fibers of the skin, the bloodvessels of the arms and legs, as well as the sweat-glands in all parts of the body.

PART VI

THE SENSE-ORGANS

CHAPTER XXXVI

THE CUTANEOUS SENSATIONS. TASTE AND SMELL

General Consideration.—We have regarded the central nervous system so far as a self-active mechanism which controls all the motor reactions of the body. In reality, however, the motor reactions are the results of diverse afferent impulses which are constantly poured into it from a number of sense-organs or receptors. The media in which animals live, are teeming with diverse manifestations of energy toward which they must orient themselves in a very precise manner in order not to endanger their existence. The reception and interpretation of these impressions is no less a duty of the central nervous system than the execution of characteristic motor responses for purposes of adaptation. Thus, the central nervous system really serves as a meeting place for diverse afferent and efferent impulses. It synthesizes afferent impressions into motor responses.

Sensations are the result of certain processes taking place within the brain in consequence of impulses derived from the distant receptors. Many sensations, however, need not be followed immediately by motor reactions, but may be stored as memory concepts and called into play at any time later without accompanying stimulations. Furthermore, sensations are specific, *i.e.*, they present different modalities in accordance with the character of the mechanism producing them. Thus, a sharp distinction should invariably be made between those derived from the retinæ of the eyes and those

relayed inward from the organ of Corti of the internal ear, although no difference is discernible in the character of the nerve impulses producing them. Consequently, the quality of the sensation must depend upon the structural and functional peculiarities of the center receiving the impulses. In analogy, the touch of an electric button need not give rise to the ringing of a bell, but may start a machine or produce light. In other words, the effect following the reception of a nerve impulse must be determined by the structural and functional character of the central organ.

The quality of the sensation is further safe-guarded by the fact that the receptor is specifically adapted to receive only one particular kind of impact. Each sensory end-organ, so to speak, can be excited by only that type of energy in space for the reception of which it is peculiarly adapted. Thus, our body may be likened to a house, the windows of which permit the entrance of light and sounds, while its walls are practically impermeable to the ordinary physical forces in space. Quite similarly, the mass of our body is invested by a relatively impervious membrane, the skin, and communicates with the outside only through particular openings in this capsular investment. Furthermore, these openings are guarded by specialized nervous mechanisms, so that the body may retain a certain independence against the energies in space and at the same time adapt its processes to the changes in the medium.

It is true that the retina of the eye may also be stimulated mechanically, chemically, and electrically, but the normal stimulus is the light ray. The former stimuli merely yield flashes of light but no distinct visual concepts. Accordingly, it may be said that the *adequate* stimulus in the case of the retina is the light ray, just as the adequate exciting agent in the case of the organ of Corti is the sound wave. All other impacts are *inadequate*, because they cannot activate the sense-organs in a normal manner.

Classification of the Sense-organs.—Man is capable of analyzing the manifestations of energy occurring in space by means of five sense-organs: namely, the retina, organ of Corti, taste-buds, olfactory cells, and tactile corpuscles.

23

The sensations mediated with the aid of these receptors are classified as sight, hearing, taste, smell and touch. It is true, however, that the sensations derived from these end-organs may be divided into a number of minor ones, and that a number of different receptors are situated in the internal structures and organs. Thus, the skin gives rise to sensations or pressure, pain, touch and temperature, while the internal ear contains not only the organ of hearing, but also that set aside for the production of the senses of position and movement. About twenty-five different sensations are perceived by us. The receptors giving rise to these may be classified as follows:

A. Somatic receptors, are concerned with the orientation of the animal toward its environment,
   1. Exteroceptors, are stimulated directly by outside forces. This group includes the retina, organ of Corti, and the cutaneous sense-organs,
   2. Proprioceptors, are concerned with equilibrium and orientation. In this group belong the sensory terminals of the muscles and tendons, as well as the semicircular canals and statocysts of the internal ear,

B. Visceral receptors or interoceptors which have to do with the sensations arising in the viscera,
   1. General interoceptors which mediate the sensations of hunger, thirst, nausea, visceral pain, as well as those perceived along the circulatory and respiratory channels,
   2. Special interoceptors which embrace the end-organs for taste and smell.

The Skin as a Sense-organ.—The skin is exposed to various influences which elicit different kinds of sensations: namely, those of pressure, touch, pain, cold, and heat. Several others, such as stroking and tickling, are composite in their character. In endeavoring to localize these sensations in definite receptors, we are confronted by the difficulty that the nerve-endings of the integument present themselves as a rule in the form of *tactile corpuscles, i.e.*, as bodies which to

all appearances are constructed for the reception of mechanical impacts. No bodies have been discovered as yet to which the sensations of temperature and pain could be singularly ascribed. The tactile receptors, on the other hand, usually exhibit a structure which leaves no doubt as to their function. They consist of a capsular investment, in the center of which lie the ramifications of the sensory nerve fibers.

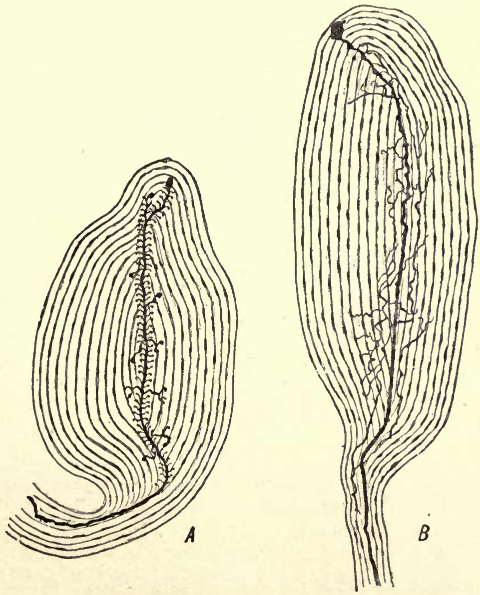


Fig. 128.—Paccinian corpuscles from the peritoneum of a cat. (*After Sala, from Böhm-Davidoff-Huber's Histology.*)

Possibly the most characteristic receiving organ of this kind is the corpuscle of Vater-Paccini (Fig. 128). It is oval in shape; about 2 to 4 mm. in length, and embraces several concentric rings. Its core is occupied by the nerve fiber. A tactile corpuscle of similar appearance is that of Herbst (Fig. 129). At the base of the bills of birds are found the corpuscles of Grandry (Fig. 130), which consist of two or more hemispheral cells, surrounded by a capsule. The spaces

between their flattened surfaces are occupied by the ramifications of the nerve fiber. While the sensitiveness of the skin varies greatly in its different regions, it has been estimated that the total number of tactile corpuscles present in man, amounts to 500,000. The skin upon the back of the leg contains about fifteen to the square centimeter.

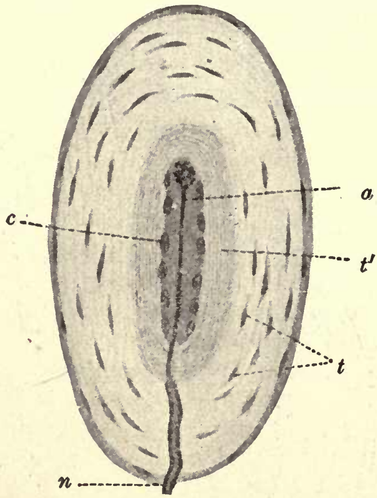


FIG. 129.—Herbst corpuscles of duck. *n*, medullated nerve-fibre; *a*, its axis-cylinder, terminating in an enlargement at end of core; *c*, nuclei of cells of core; *t*, nuclei of cells of outer tunica; *t'*, inner tunica × 380 diameters. (*Sobotta*)

The structure of these sense-organs makes it evident that their stimulation results in consequence of mechanical impacts, causing a displacement of the deeper layers of the skin. The pressure brought to bear upon their capsular investments is communicated in some inexplicable manner to the nerve terminals. Nerve impulses arise in consequence of these impacts which then receive their proper interpretation in the corresponding cerebral center. These cutaneous sensations are generally referred to the place in which they originate, while those pertaining to sight and sound are projected into space. Thus, a visual sensation is not associated as com-

ing from the retinæ of the eyes, but as arising in space. A similar projection, however, may at times be experienced even with the cutaneous receptors. Thus, if the point of a knife is moved across a rough surface, the grating sensation does not appear to be derived from the skin, but from the line of contact between the knife and the object.

Painful sensations may be obtained by the stimulation of practically any sense-organ. This is true of obnoxious odors, loud sounds, and high intensities of light. The ordinary

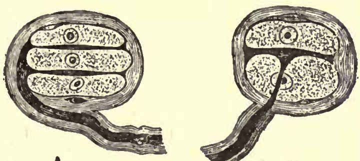


FIG. 130.—Corpuscles of Grandry from the duck's tongue. *A*, compound of three cells, with two interposed discs, into which the axis-cylinder of the nerve, *n*, is observed to pass; in *B* there is but one tactile disc enclosed between two tactile cells. (*Izquierdo.*)

cutaneous sensation of pain, however, results either in consequence of the excessive stimulation of the ordinary receptors for touch or in consequence of the excitation of specialized nerve-endings. The latter view is commonly accepted today, although the structural details of these receptors are not known.

The integument also embraces a series of sensory points which yield distinct sensations of cold or heat. The cold spots are more numerous than the heat spots, their relationship being as 13 : 1.5. Between these areas giving positive reactions, are situated fields of different size which do not give distinct sensations of temperature. The acuity of this sense varies greatly in different regions of the body. It is less in the midline of the body than in its lateral regions.

The Sense of Taste.—The end-organ mediating the sense of taste, is the taste-bud, so called because its cellular elements are arranged somewhat like the leaves of a bud. It measures 80μ in length and 40μ in breadth, and appears as a flask-shaped cavity which is filled with closely packed

elliptical cells. This small depression in the mucosa communicates by means of a porous opening with the general cavity of the mouth, while its inner pole receives the terminals of the nerve fiber (Fig. 132).

In children, the taste-buds are widely distributed upon the upper surface of the tongue, and the lining of the fauces, walls of the pharynx, and cheeks. In adult life, on the other hand, they disappear from the outlying regions and remain

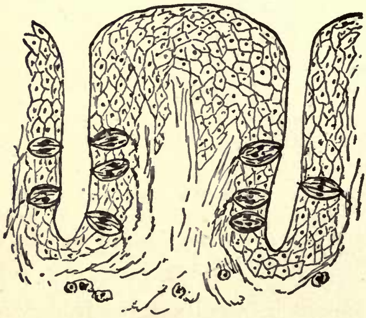


FIG. 131.

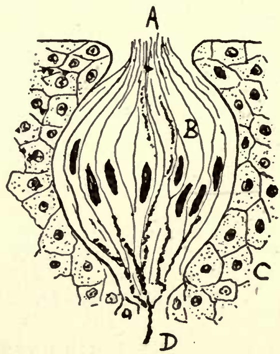


FIG. 132.

FIG. 131.—Diagrammatic representation of circumvallate papilla showing the position of the taste-buds.

FIG. 132.—Transverse section through a taste-bud. *A*, taste pore; *B*, spindle-shaped cells of the taste-bud; *C*, reticular cells; *D*, nerve fibres terminating among its cells.

more closely confined to the tongue and fauces. Their wide distribution explains the fact that several nerves are concerned in conveying the gustatory impulses to the corresponding cerebral center. Those most directly involved are the lingual, a branch of the inferior maxillary division of the fifth cranial, the glossopharyngeus, and the vagus.

Upon its entrance into the mouth, the food is subjected to a mechanical as well as chemical reduction. The saliva plays the part of a solvent, because substances to be tasted must be in the fluid state. In this condition they are able to penetrate into the crevices between the papillæ of the tongue and to form contact with the pointed ends of the gustatory

cells. It should be noted that the tongue does not possess a perfectly smooth surface, but is beset with many minute papillæ which are either pointed or rounded at their apices. In the crevices between these elevations lie the taste-buds in varying numbers: sometimes one, sometimes several being situated in one of these pockets (Fig. 131).

It is also to be noted that these sense-organs are specific in their function, and give rise to only one particular kind of taste sensation. Sweet is most keenly perceived upon the tip, and bitter upon the back of the tongue. The other modalities, namely, sour and salty, are perceived best upon the lateral and antero-lateral regions of this organ.

The Sense of Smell.—The nasal cavity is lined throughout with mucous membrane containing a large number of glands of the ordinary lubricating variety. One particular area of it, however, embraces not only reticular cells but also cells representing the modified sensory terminals of the nerve of smell or olfactory nerve. These cells exhibit a spindle-like shape; moreover, their outer tips are beset with hair-like projections which protude somewhat beyond the general surface of the lining membrane. The odoriferous particles contained in the respiratory air are brought in contact with these projections, and in some way activate the substance of the neighboring olfactory epithelium. The resulting impulses are relayed from here to the corresponding cerebral center.

The two nasal chambers are separated from one another by a median partition, formed by the vomer and adjoining cartilaginous septum. Directly above the bony palate separating the nasal cavity from that of the mouth, lies a relatively large channel through which the respiratory air ebbs back and forth between the nostrils and the posterior nares. This particular region of each nasal chamber is known as the *regio respiratoria*.

The remaining extent of each chamber is subdivided into many spaces by the upper, middle, and lower turbinated or spongy bones which project diagonally into the lumen of the main cavity. The surfaces of these delicate partitions are covered with ordinary mucous membrane. The upper

extent of the median septum and opposing surfaces of the upper and middle turbinated bones, however, contain in addition to the reticular lining the aforesaid olfactory cells. The term: *regio olfactoria* has been applied to this particular area of the nasal cavity. It measures about 250 sq. mm. on each side, and equals, therefore, the cross-area of a five-cent piece.

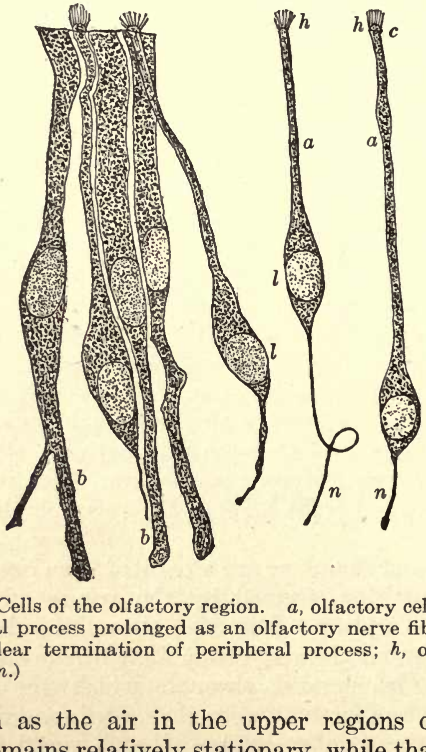


FIG. 133.—Cells of the olfactory region. *a*, olfactory cells; *b*, epithelial cells; *n*, central process prolonged as an olfactory nerve fibril; *l*, nucleus; *c*, knob-like clear termination of peripheral process; *h*, olfactory hairs. (*After v. Brunn.*)

Inasmuch as the air in the upper regions of the nasal chambers remains relatively stationary, while that traversing their lower portions moves constantly back and forth, it must be concluded that the odoriferous particles contained in the latter slowly diffuse upward until they reach the olfactory areas. Accordingly, it will be seen that a certain time must elapse between the entrance of these particles into the nasal passages and the moment when they are able to produce

their characteristic effect upon the olfactory cells. This latent period may be shortened considerably by the act of sniffing which causes the air suddenly sucked in through the nostrils to be diverted upward into the olfactory chamber. It replaces here the air just drawn into the pharynx. The structural and functional peculiarities of this mechanism make it evident that a severe cold which is characterized by a swelling of the mucous membrane, must give rise to an occlusion of these narrow spaces and impair the diffusion of the odorous particles. It should also be remembered that such agents as ammonia irritate the nasal mucosa and excite the receptors of the trigeminal nerve rather than those of the olfactory area.

CHAPTER XXXVII

THE SENSES OF HEARING AND EQUILIBRIUM

The External Ear.—Sound waves are vibrations in the material medium of air. They arise in consequence of movements of elastic bodies. Thus, if a metal plate is suspended and is struck near its center with the end of a rod, its constituent elements will be displaced in the direction of the stroke. Having attained an extreme position in this direction, they will then seek to recover their original contours and places, causing the plate to become convex on the side of the impact. These lateral deviations will be repeated a number of times until the entire system has again entered the resting state. While the plate changes its shape, the air resting upon its two surfaces is alternately put under a high and low pressure, *i.e.*, the air lying in contact with its convex surface is compressed, whereas that upon its concave surface is rarefied. In this way, a series of progressive undulations are produced in the air in harmony with the elastic qualities of the vibrator. Some of these waves are large in amplitude and others small, and hence, it may be said that they represent a varying rapidity of vibration of the air. The greater the number of these vibrations, the higher the *pitch* of the sound. The vibratory peculiarities of the elastic body determine the *quality* of the sound, while its *intensity* or *loudness* is occasioned by the amplitude of the vibrations of the sonorous body.

When a sound is produced near at hand, it seems to reach consciousness almost instantaneously. We well know, however, that sounds require a certain period of time for their transmission through the air, as well as for their passage through the ear. Thus, a distant locomotive is seen to discharge steam through its vibrator many seconds before the sound produced thereby is actually perceived, and the

lightning is seen several moments before the thunder is heard. In air, the speed of the sound-waves is 340 m. in a second, but other media conduct it with an even greater rapidity. Thus, water transfers it with a velocity of 1450 m. in a second and wood at a speed of 13,000 m. in a second.

As these waves reach the external ear, they are received by its funnel-shaped *pinna* and *concha*, and are then reflected into the orifice of the *external auditory canal*. It is true,

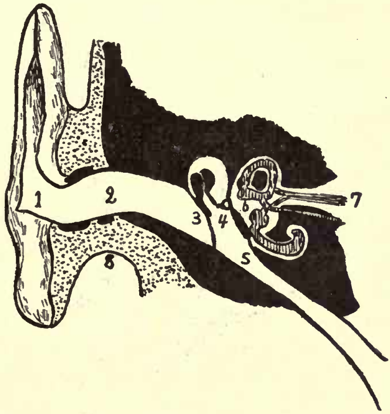


FIG. 134.—Diagrammatic representation of the different parts of the ear. 1, pinna; 2, external auditory meatus; 3, ear drum; 4, middle ear containing the ossicles; 5, Eustachian tube; 6, vestibule of the internal ear; 7, auditory nerve; dividing into two branches, one of which innervates the cochlea and the other, the semi-circular canals; 8, parotid gland.

however, that the pinna plays a rather unimportant part in the reception of sounds, because many animals are not in possession of an appendage of this kind and nevertheless display a keen sense of hearing. Likewise, a person whose pinna has been removed, does not reveal any indications of an impairment in his hearing.

The waves of sound traverse the external auditory canal and finally impinge upon a membrane which is placed obliquely across its inner lumen. This is the *ear drum* or *tympanic membrane*. It consists of a cartilaginous ring, across which is stretched a layer of fibrous tissue covered

on its outer side with delicate skin, and on its inner side with mucous membrane. It possesses a somewhat oval shape, and measures 10 mm. in height and 8 mm. in width. Its area measures 50 sq. mm.

The function of the ear drum is to receive the sound waves entering through the external auditory canal, and to vibrate in harmony with them. Furthermore, in order that this

FIG. 135.—Diagrammatic representation of the middle ear or tympanic cavity. 1, external auditory meatus; 2, the ear drum or tympanic membrane; 3, malleus, with its manubrium resting against the internal surface of the ear drum; 4, incus; 5, stapes resting against the membrane of the fenestra ovalis; 6, vestibule of the internal ear; 7, fenestra rotunda, 8, Eustachian tube; 9, saccule; 10, central canal of the cochlea; 11, utricle; 12, musc. tensor tympani.

membrane may be adapted to waves of different amplitude, its tenseness is constantly altered by a muscle which is attached to its inner surface through the medium of the hammer-bone. This muscle is known as the *tensor tympani.*

The Middle Ear.—When we pass beyond the ear drum which closes the inner orifice of the external auditory canal, we reach the *cavity of the middle ear* or *tympanic cavity,* in which are situated the *ear bones* or *ossicles.* They are three in number: namely, the hammer bone or malleus, the anvil bone or incus, and the stirrup bone or stapes. This entire cavity is filled with air, and communicates with the outside

only through a relatively long and narrow membranous passage, the *Eustachian tube.* The orifice of this channel is situated upon the posterior wall of the pharynx. The inner wall of the cavity of the middle ear is formed by a bony septum which bears two orifices: namely, the *fenestra ovalis* and *fenestra rotunda.* Both openings are closed by membranes. Inside this partition lies the *cavity of the internal ear* which is filled throughout with a lymphatic fluid and contains the most important element of the mechanism of hearing, namely, the *organ of Corti.*

This structural arrangement leads us to assume that the vibrations in air must first be converted into vibrations of lymph before the aforesaid receptor, the organ of Corti, is able to receive them. Keeping this fact clearly in mind, it may then be concluded that the only function of the structures of the middle ear is to accomplish this transfer of the sound waves into vibrations in lymph. It has been noted above that the waves transmitted through the air give rise to an oscillation of the drum of the ear. Clearly, in order to produce similar oscillations in the lymph of the internal ear, the membrane closing the fenestra ovalis must be made to vibrate synchronously with the ear drum. In other words, every impact upon the latter must evoke a corresponding movement of the lymph in the internal ear. The question pertaining to the manner in which the ear drum is able to produce corresponding displacements of the membrane closing the fenestra ovalis, and vibrations in lymph, is easily answered by a brief examination of Fig. 135.

It will be seen that the ossicles are arranged in series, and are freely suspended in the cavity of the middle ear by ligamentous bands. The long process of the hammer bone lies in firm contact with the inner surface of the ear drum and must, therefore, oscillate in harmony with this membrane. It is moved back and forth like the pendulum of a clock. Since the neck of this bone is held in position by two ligaments, its head must always move in a direction opposite to that of its process. Furthermore, inasmuch as the head of the malleus is joined with the incus by a broad articulation, the movements of the latter must conform to those of the

former. Owing, however, to a peculiar arrangement of the centers of rotation of these bones, the stapes which is attached to one of the processes of the incus, is moved inward whenever the process of the malleus is forced inward, and vice versa. In this way, every movement of the ear drum is enabled to leave its impression upon the membrane of the fenestra ovalis.

A proper oscillation of the ear drum can only be effected if the pressure upon its two sides is equal. This end is attained by repeated interchanges of air between the cavity of the middle ear and that of the pharynx. The Eustachian tube to which reference has already been made above, is the means by which this equalization of the pressures is accomplished. It is a matter of common experience that a high atmospheric pressure, such as we are often exposed to while traversing a tunnel, causes the ear drum to bulge inward, thereby diminishing its power of vibration and lessening the acuity of the sense of hearing. The peculiar sensations of pressure then experienced, may readily be remedied by the act of swallowing, because the contraction of the constrictors of the pharynx opens the orifice of the Eustachian tube and permits air to enter the cavity of the middle ear. As soon as the pressures upon the two sides of the ear drum have been equalized, it acquires its former power of vibration. It need scarcely be mentioned that a rarefication of the outside air causes the ear drum to deviate outward. The opening of the Eustachian orifice then permits air to escape from the cavity of the middle ear.

This brief discussion makes it evident that a severe cold implicating the mucous lining of the pharynx and Eustachian tube, must greatly impair this interchange of air. For this reason, a certain loss of the acuity of hearing is not an uncommon result of this affection. Attention should also be called at this time to the fact that septic inflammations of this membranous tube may implicate the mucous lining of the tympanic cavity, and eventually give rise to a perforation of the ear drum. As long as such a defect is not established in the immediate vicinity of the handle of the malleus, it need not impair the vibratory power of the ossicles. Furthermore,

the close proximity of the cellular spaces of the mastoid process of the temporal bone constitutes a constant danger, because any inflammatory process affecting the middle ear, may spread into them and eventually give rise to a perforation into the cranium. In this eventuality, the inflammation usually extends very rapidly along the coverings of the brain.

The Internal Ear.—In order to be able to understand the functions of the internal ear, it should be noted first of all

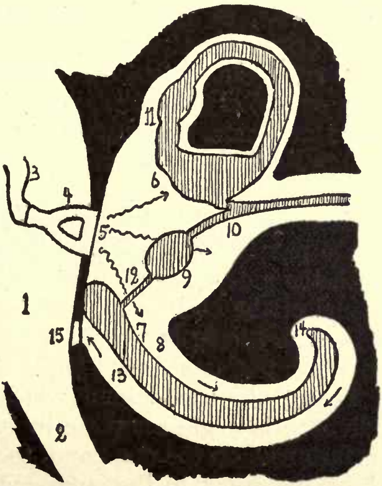


Fig. 136.—Diagrammatic view of the internal ear. 1, tympanic cavity; 2, Eustachian tube; 3, incus; 4, stapes; 5, vestibule of the internal ear (perilymph); 6, utricle; 7, central canal of the cochlea; 8, scala vestibuli; 9, saccule; 10, endolymphatic duct between saccule and utricle; 11, ampulla of semicircular canal; 12, canalis reuniens; 13, scala tympani; 14, helicotrema; 15, fenestra ovalis.

that this structure presents itself as a small cavity in the petrous portion of the temporal bone which is filled with lymph. In this lymph floats a membranous canal which is almost an exact reproduction of the bony cavity. The lumen of this membranous tube is also filled with lymph. Accordingly, any cross-section of the internal ear presents first of all an outer wall of bone; then, a layer of lymph which is termed *perilymph;* next, the wall of the membranous tube;

and lastly, the core of lymph within the latter which is called *endolymph.*

It should also be noted that the internal ear contains not only the receptor for the sound waves or organ of Corti, but also one concerned with the production of the sense of equilibrium and situated in the ampullæ of the labyrinth. Thus, the internal ear may be divided into two distinct parts: namely the *cochlea,* in which is located the organ of Corti mediating the sensations of hearing, and the *saccule, utricle and semicircular canals,* in which those sensations arise which enable us to orient ourselves in space.

The *cochlea* is a snail-like structure situated anteriorly to the vestibule (fen. ovalis) of the internal ear. It measures 9 mm. across its base and 5 mm. from base to apex This bony tube is wound upon itself two and one-half times, and contains a membranous tube which is closely adherent to its wall in several places, so that its lumen becomes subdivided into three separate passages. This arrangement may best be illustrated with the aid of Fig. 137, representing a cross-section of the canal of the cochlea at practically any level. It will be seen that its lumen is partially divided into two by a bony plate which projects almost horizontally outward from the central core of bone around which the canal is wound. This division is made complete by a membranous septum which is fastened, on the one hand, to the tip of this bony plate and, on the other, to the outer wall of the canal. It is called the *basilar membrane.* Above this septum lies the *scala vestibuli,* so-called because it leads from the region of the fenestra ovalis or vestibule of the internal ear into the tip of the cochlear canal, a distance of about 33 mm. Below this septum lies the *scala tympani* which is connected with the former in the tip of the canal and terminates blindly at the fenestra rotunda.

It is to be noted especially that the scala vestibuli and scala tympani are perilymph canals. The endolymph canal is represented by the *central canal,* the floor of which corresponds to the aforesaid membranous septum, while its roof is formed by a delicate membrane which stretches obliquely through the vestibular scala. The latter is termed

the *membrane of Reissner.* The lining of the upper surface of the basilar membrane is modified to give lodgment to the terminals of the auditory nerve. The cells assume here a peculiar shape and acquire hair-like processes upon their

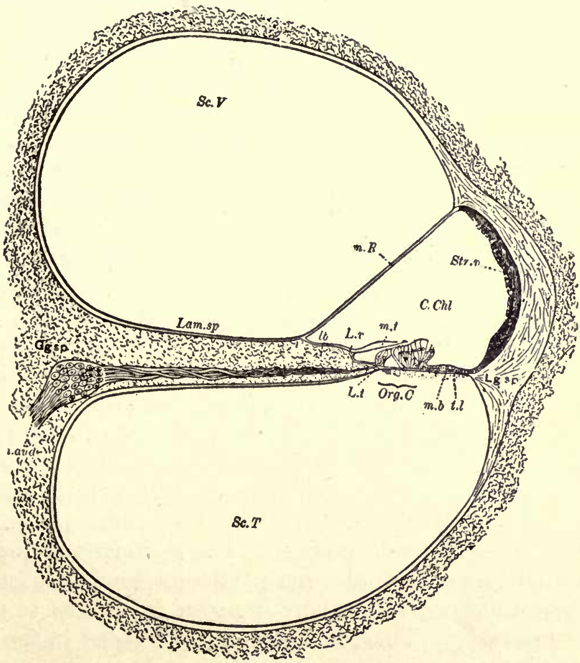


FIG. 137.—Diagram of a transverse section of the cochlea. *Sc. V*, scala vestibuli; *Sc. T*, scala tympani; *C. Chl*, canalis cochlearis; *Lam. sp.*, lamina spiralis; *Gg. sp*, ganglion spirale; *n. aud*, auditory nerve; *m.R*, membrane of Reissner; *Sv.tr.* stria vascularis; *Lg.sp*, ligamentum spirale; *t.l*, lymphatic epithelioid lining of basilar membrane on the tympanic side; *m. b*, basilar membrane; *Org. C*, organ of Corti; *L.t*, labium tympanicum; *lb*, limbus; *L.v*, labium vestibulare; *m.t*, tectorial membrane. (*After Foster.*)

outer surfaces which project free into the lymph of the central canal. These hair cells, together with a number of reticular cells, constitute the *organ of Corti* which is responsible for the reception of the sound waves.

The manner of activation of this receptor may be briefly outlined as follows: The impacts of the stapes upon the membrane of the fenestra ovalis, executed in harmony with the vibrations of the ear drum, give rise to vibrations in the perilymph of the internal ear. The latter ascend through the scala vestibuli and descend through the scala tympani. This implies that the membrane closing the fenestra ovalis must vibrate synchronously with the membrane of the fenestra rotunda, but in opposite directions to one another. In this way, certain interchanges of pressure are effected which permit the membrane of the fenestra ovalis to oscillate with the greatest possible freedom. Since the endolymph of the central canal in which the organ of Corti is situated, is separated from the perilymph in the vestibular scala by only a very thin membrane, the vibrations of the latter are easily communicated to the former. It appears, that the vibrations in the endolymph then evoke movements of the hair-like processes upon the cells of Deiters which in some way activate the terminals of the auditory nerve.

It is obvious, therefore, that the hair-cells of the organ of Corti play the part of resonators. As such they are able to analyze the different vibrations in lymph, corresponding in turn to the varying amplitudes of the sound waves. The action of these hair-cells is specific, *i.e.*, any given cell appears to be able to receive only one particular kind of vibration. The general phenomenon here involved is familiar to practically everybody. Thus, if a sound is produced in the vicinity of a string-instrument, only that string will be set into sympathetic vibration by it which is structurally adapted to receive it. The total number of hair-cells is usually given as 16,000, a number sufficient to allow us to analyze musical sounds of between 16 and 30,000 vibrations per second. In fact, the trained musical ear is able to recognize even sounds of 50,000 vibrations per second.

The Semi-circular Canals.—In many of the lower animals the organ of equilibrium consists merely of a saccular indentation of the integument which is lined with cuboidal cells possessing hair-like projections. The ends of these filaments are often weighted with minute calcareous concretions which

are known as otolyths. A peculiar semi-liquid material occupies the remaining portion of this cavity. This entire structure is termed a *statocyst*, or *otolithic cavity*, and its function is to mediate the static sense or sense of position. The animals, possessing end-organs of this character, move principally along straight lines and are not subjected to rotary movements; hence, a simple receptor of this kind is really all they require in order to be able to ascertain their position in space. It is evident that any change in the position of the head of the animal must cause the hair-like projections of the lining cells of the statocysts to be deviated in consequence of the changes in the pressure of the material overlying them. These deviations activate the sensory fibers connected with the basal portions of these cells. Sensory epithelium of this kind is also present in the human ear, but only in the utricular portion of the membranous canal.

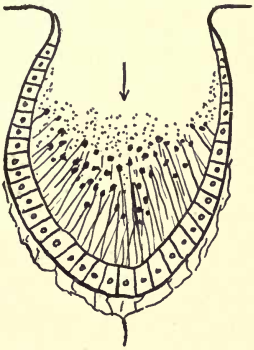


FIG. 138.—The otolithic cavity showing the lining cells with their hair-like prolongations and the otoliths.

The principal receptor mediating sensations of position lies in the *ampullæ* of the semicircular canals. If we pass backward from the vicinity of the fenestra ovalis, we find that the bone is hollowed out in the form of three narrow canals, each describing a half-circle. Inside these lie membranous tubes of the same general shape which begin and terminate at the utricle, a spacious enlargement of the endolymph sac. Within a short distance of the utricle, each semicircular canal presents a bulbular enlargement, which is termed the *ampulla*. The lining of this particular segment of the canal is raised in the form of a transverse ridge, and is made up of high cells bearing hair-like projections which float free in the endolymph. This structure is known as the *crista acustica*. It is supplied by fibers from the vestibular branch of the auditory nerve.

It should be noted next that these canals are arranged in

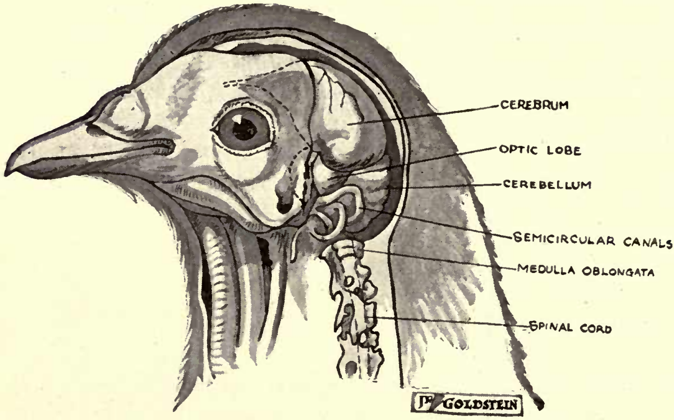


FIG. 139.—The semicircular canals in the pigeon.

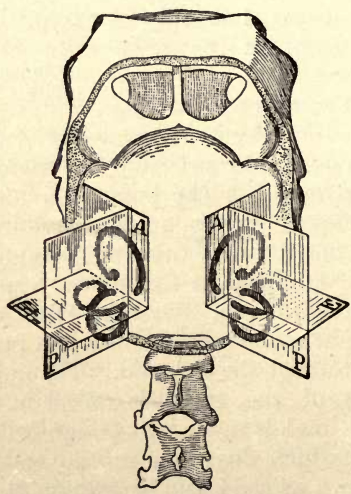


FIG. 140.—Figure showing the position of the three semicircular canals in the skull of the pigeon. (*Ewald.*)

such a way that they cover three distinct planes in space, situated approximately at right angles to one another. One canal is placed horizontally, while the other two are directed vertically when the head is held erect. The two vertical canals deviate from the mesial plane at an angle of 45°; hence, if the positions of the right and left canals are compared with one another, it will be found that the left anterior covers the same plane as the right posterior. Quite similarly, the right anterior is supplemented by the left posterior. Movements in any direction not in line with the planes of these canals activate two canals in an unequal measure.

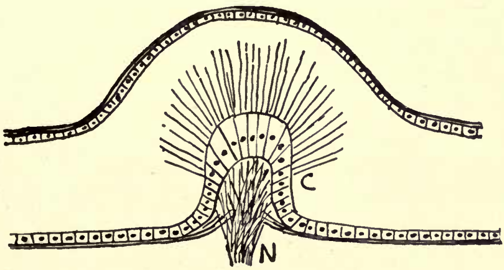


Fig. 141.—Diagrammatic representation of the structure of the ampulla of a fish. The columnar cells of the crista acustica (*c*) are beset with hair-like prolongations which float free in the endolymph. *N*, nerve fibers leading away from ampulla.

The fact that these structures are intimately concerned with equilibration has been amply proven, because their destruction gives rise to disorders in the power of retaining our position. The birds are especially adapted for experiments of this kind, because their labyrinth is very accessible to operative interference. Thus, a pigeon whose canals have been extirpated on one side, is quite unable to maintain its position. If it is made to move, it sways and tumbles toward the side of the injury. Its head is tilted toward one side and may even be inverted. A certain adjustment, however, takes place in the course of time, so that an animal of this kind will not show such serious disturbances when allowed to remain relatively quiescent.

The manner of activation of this receptor may readily be deduced from its histological structure. Whenever the head is moved in a particular direction, the lymph within the membranous canal is also moved, thereby causing the hair processes to be deviated from their position of rest. Although gravity cannot be excluded altogether, it is evident that this receptor is peculiarly adapted to movements and mediates, therefore, the *dynamic sense*. In man, the purely static sensations are believed to be received by the sensory epithelium of the utricle and saccule.

CHAPTER XXXVIII

THE SENSE OF SIGHT

The Nature of the Stimulation by Light.—The sources of light are either natural or artificial. In the former group belong the sun, stars, comets, meteors, and phosphorescent bodies, and in the latter the combustions of gas, oil, wood, coal, and other substances. Regarding the cause of light, two theories have been propounded which are characterized respectively as the *emission* or *corpuscular* and the *undulatory*. The former regards light as minute particles which are discharged by the luminous body in straight lines, while the latter assumes that combustions give rise to vibrations in ether, the attenuated medium filling space. These vibrations are propagated with an almost inconceivably rapid rate, usually estimated at about 190,000 miles in a second.

In their passage through space these vibrations are brought in contact with different bodies, which are classified as: *transparent*, when they permit the passage of white light and its spectral components so that the object may be seen in its colors: *translucent*, when only a certain number of rays are able to pass outlining the object as a shadow, and *opaque*, when the rays cannot get beyond them. Furthermore, an opaque body may cause a certain number of the rays to be absorbed and another to be reverberated. In the latter case, the light changes its direction, although continuing in the same medium. The term of *reflection* is applied to this phenomenon. If a ray of light is made to pass from one medium into another in an oblique direction, it is deviated from its course. This phenomenon is characterized as *refraction*.

Light is the most potent stimulant of living matter. The lowest forms require it in optimum intensities. Any greater or lesser amount acts destructively upon them. Thus we

find that such organisms as the amœba behave toward it in a particular manner, being attracted to it when its intensity is low, and repelled when its intensity is high. In other words, these organisms orient themselves toward light in a positive as well as negative manner, but in all these instances the stimulus is brought to bear upon their substance in a direct way and in all probability not through special receiving organs. Furthermore, the effects of these impacts are limited to changes which give rise solely to particular movements. The term of *heliotropism* or *phototaxis* is applied to the power of simple organisms to orient themselves in accordance with the intensity and direction of the light rays.

Somewhat higher in the scale of the animal kingdom, we note the development of the so-called eye-spots, which first appear in the form of globules of a peculiar substance extremely sensitive to light. But even this receptor substance does not seem to mediate anything more complex than the estimation of varying degrees of light: *i.e.* distinct imprints of objects cannot be obtained with the aid of this material. In the higher invertebrates, the sensitive epithelium is spread out in the form of a hemispherical layer and is invested by structures, the principal purpose of which is to bring the rays of light to a concise intersecting point upon it. Thus, the eye of the insects presents numerous funnel-shaped tubes through which the light is refracted by means of delicate lenses of chitin. This type of eye, however, is soon abandoned and gives way to one possessing a single system of curved refracting media. It thus acquires a striking similarity to a camera obscura, the box of which is represented by the wall of the eyeball, its refracting medium by the cornea and lens, and its sensitive screen by the retina.

Naturally, the most important constituent of the eye is its sensory epithelium, because it permits the transfer of the ethereal vibrations into sensations of light which are then relayed to the corresponding center in the cerebrum to be associated. Thus, the cornea, lens, and humours of the eye should be regarded merely as adjuncts, by means of which the rays of light are centralized upon this receptor in the most efficient manner. In this connection, it should also be men-

tioned that this receptor may be excited by mechanical and electrical stimuli, but these impacts give rise solely to sensations of light which are commonly known as phosphenes, and not to distinct reproductions of outside conditions. Associative imprints are formed only in consequence of stimulations by light. Accordingly, the only adequate stimuli in the case of the retina are the ethereal vibrations.

The General Structure of the Eye.—The organ of sight is arranged in a bilateral manner. It consists of two globular

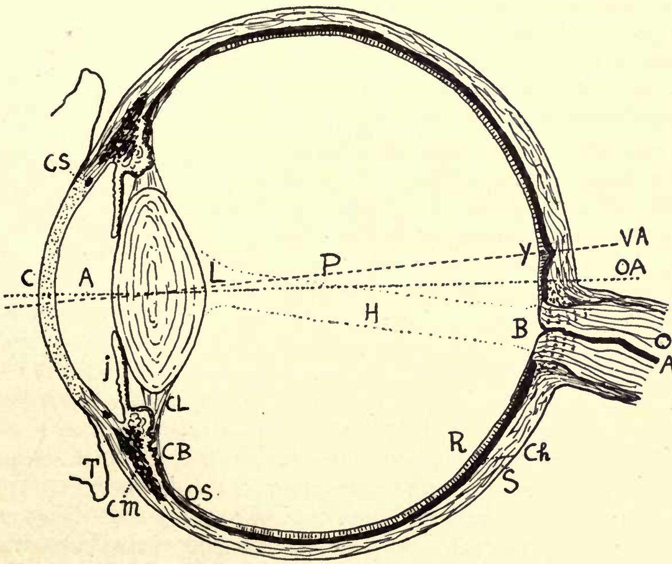


FIG. 142.—Diagram of a horizontal section through the human eye, *C*, cornea; *A*, anterior cavity; *P*, posterior cavity; *L*, lens; *J*, iris; *T*, conjunctival sac; *CL*, ciliary ligament; *CB*, ciliary body; *CM*, ciliary muscle; *OS*, ora serrata; *CS*, canal of Schlemm; *R*, retina; *Ch*, choroid; *S*, sclera; *ON*, optic nerve; *A*, retinal artery; *B*, blind spot; *Y*, yellow spot; *OA*, optical axis; *VA*, visual axis; *H*, hyaloid canal.

bodies, the eyeballs, which are situated in the orbital cavities of the skull. Each eye ball is invested by a capsule, the surfaces of which are moistened with a lymphatic fluid to facilitate its movements. In front it is protected by the eyelids

which appear primarily as reflections of the skin, covering almost one-half of its entire outer surface. Those regions of the lids which lie in relation with the eyeball, are lined with mucous membrane and are constantly moistened with a watery fluid, secreted by the lacrimal gland. This structure is placed in a depression in the horizontal plate of the frontal bone above the outer corner of the cleft between the lids.

After this secretory product has been discharged into the conjunctival sac, it is spread by capillarity across the surface of the eyeball, thereby tending to keep the latter from drying and to remove from it all particles of dust that may have accumulated upon it. The tears finally escape from the conjunctival sac through two small openings in the inner angles of the lids. They then enter the nasal cavity by way of the nasal duct, the orifice of which is situated in the upper portion of this recess. Thus, lacrimation must always be followed by the escape of an extra amount of fluid from this passage. Under ordinary conditions, the tears do not flow across the edges of the lids, because the inner margins of the latter are equipped with a large number of modified sebaceous glands, secreting an oily liquid. These are the *Meibomian glands*. Their oily product also serves as a lubricant for the hairs with which the outer margins of the lids are beset as a means of protecting the eyeball against dust.

The wall of the eyeball is composed of three layers of tissue: namely, a dense outer covering or *sclera*, a delicate vascular layer or *choroid*, and an inner coat of sensory epithelium or *retina*. The strength and resistance of the eyeball are due, of course, to its connective tissue envelope in the form of the sclera, while its nutrition is effected chiefly by the vessels of the choroid. Within this rounded capsule the retina is expanded in the form of a hemispherical funnel, its concave surface being directed toward the anterior pole of the eyeball, while its convex posterior surface lies everywhere in intimate contact with the choroid. The nerve fibers of the retina strive radially toward a common center and leave the eyeball near its posterior pole in the form of the optic nerve.

The retina, as well as the choroid, covers the sclera for

only about three-fourths of its extent. Furthermore, at about the line of junction between the anterior one-fourth and posterior three-fourths of the eyeball the sclera becomes transparent. This permeable segment of this fibrous capsule is named the *cornea.* It is more convex than its opaque posterior part, so that the eyeball as a whole really possesses the shape of two telescoped spheroids, its corneal vestibule being cut out of a smaller, and hence, more convex sphere.

If we now observe the eyeball in longitudinal section, it will be seen that its external characteristics correspond very closely to its internal structure. It is to be noted first of all that its cavity is subdivided into an anterior and a posterior chamber by a vertical partition consisting of the *ciliary body, lens* and *iris.* Both chambers are filled with fluid, that in the anterior compartment exhibiting the consistency of lymph, and that in the posterior cavity the consistency of a delicate jelly. The former is designated as *aqueous humour,* and the latter, as *vitreous humour.* It is to be noted especially that these fluids are held under a certain pressure, tending to keep the different membranes and partitions of the eyeball fully expanded, so as to obtain the best possible refraction of the rays of light

The External Muscles of the Eyeball.—In order to be able to bring the rays of light emitted by objects in space to a precise focal point upon the retinæ, it is essential that the eyeballs be moved in the direction of the object by local muscular action. Any additional deviation that may be needed to accomplish this end, is attained by moving the head and body as a whole. The muscles of the eyeball originate upon the walls of the orbital cavity in the vicinity of the optic foramen, and pass forward to be inserted upon the eyeball back of the cornea. They are six in number: namely, four straight ones and two oblique ones. The first are designated respectively as the superior, inferior, external and internal recti muscles, and the latter, as the superior and inferior oblique muscles.

Inasmuch as the eyeball is moved in a capsule around its horizontal, vertical and oblique axes, it is evident that the contraction of the superior rectus turns the cornea upward, while that of the inferior rectus turns it downward.

Quite similarly, the external rectus deviates the long axis of the eye outward. The reverse position is given to it by the contraction of the internal rectus.

The action of the upper oblique muscle is easily understood if it is remembered that its tendon traverses a pully-like loop before it is actually inserted upon the outer aspect of the eyeball somewhat behind its center. Owing to the peculiar course followed by this muscle, its contraction must turn the cornea downward and inward. The lower oblique muscle arises from the anterior margin of the orbital cavity externally to the orifice of the nasal duct, and passes backward, outward, and upward to be inserted into the outer sclera. It turns the cornea upward and inward.

It is usually believed, however, that the oblique muscles do not act singly but only in conjunction with the recti muscles. Furthermore, the innervation of the muscles on the two sides is adjusted in such a way that the object is focalized upon harmoneous areas of the retinæ. Thus, when gazing at a near point, the eyes are converged equally by the internal recti muscles, so that the rays of light emitted by this object fall upon corresponding points of the retinæ.

CHAPTER XXXIX

THE COURSE OF THE RAYS OF LIGHT THROUGH THE EYE

The Cornea and Aqueous Humour.—Any luminous point in space emits rays of light radially in all directions. A certain number of these always pursue a course parallel to the long axis of the eyeball, provided the object is situated at a distance of at least 5 to 6 m. As these rays impinge upon the cornea, they are refracted, because this medium possesses a much greater density than the air. Similar deviations of the rays are effected at other lines of contact between the different media of the eyeball, the tendency always being to converge them into a precise intersecting point upon the retina. As the different luminous points of an object are focalized in this way upon this screen, they attain definite values as lights and shadows and even as colors which are then properly associated in the corresponding center of the cerebrum.

The cornea, therefore, plays the part of a converging plane which directs the rays of light into the eye. Thus, many of those which strike its surface slantingly and would therefore be lost, are deviated sufficiently from their course to allow them to reach the interior of the eye. Having traversed the aqueous humour, the rays are rendered strongly convergent by the crystalline lens.

The Iris.—It should be noted, however, that only those rays actually reach the lens which traverse the central area of the cornea, because only these are able eventually to engage in the pupillar orifice of the iris. A glance at Fig. 142 will show that the lens is protected in front by a thin membranous diaphragm which possesses the same purpose as the stop of a photographic camera. This statement implies that the opening between its margins may be altered in size, thereby permitting varying numbers of light rays to enter the interior of the eyeball. Thus, only the centralmost segment of the

crystalline lens is actually exposed to the light, while its outer area is covered by the iris. This is of greatest importance, because it is a well established fact that the central portion of a convex lens refracts most perfectly. Contrariwise, its peripheral segments are prone to converge the rays in different directions, so that caustics are formed. It may be said, therefore, that the iris possesses two functions: namely, that of varying the size of the bundle of light which is permitted to stimulate the retina, and that of directing the rays through the most perfect central area of the lens.

These changes may easily be observed in any person when he is requested to gaze alternately at a bright light and a dark wall. In the former instance, the pupil becomes smaller, so as to protect the retina against the entrance of an excessive number of light rays. It will be remembered that the constriction of the pupil is caused by the contraction of a group of smooth muscle cells which traverse the substance of the iris in a circular direction, while the enlargement or dilatation of this orifice is accomplished by the contraction of its radial muscle fibers and consequent retraction of the margins of the iris.

Naturally, the pupil of the eye must appear dark to the observer, because the back of the eye is not luminous, and hence, cannot emit rays of light which are projected outward through this orifice. It can be rendered luminous, however, by reflecting light into the eye by means of a mirror. Having in this way lighted up the retina or fundus of the eye, a large number of luminous points are formed which send rays outward into space. These are then focalized in the observer's eye. Furthermore, the iris itself is practically impermeable to the rays of light, because it contains a certain amount of pigment, which lends color to the eye as a whole. The heavier this deposit, the darker its color. Consequently, the blue color of the iris signifies that it embraces a smaller amount of pigment than one giving the sensation of brown. The eyes of albinos are deficient in pigment and, hence, these persons endeavor to shield the retinæ against an excessive stimulation by the light rays by partially closing the eyelids. Furthermore, an eye of this

character appears pink, because it allows a large number of reflected rays to pass outward into space.

It need scarcely be emphasized that the constriction and dilatation of the pupil cannot be effected volitionally. Both are reflex acts, instituted by the excitation of the light rays. Those changes which result in consequence of variations in the intensity of the rays, constitute the so-called *light-reflex*. Very similar alterations are noted when the eye is alternately fixed for far and near objects. In the latter instance, the pupil becomes smaller in order to restrict the size of the bundle of light. Contrariwise, it is a requirement of distinct far vision that every available ray be permitted to enter the eyeball. Consequently, the pupil is dilated at this time. These changes constitute the so-called *accommodation-reflex*.

The Lens and Ciliary Body.—While the contents of the eyeball are adjusted in a manner to act as a biconvex lens, the principal refraction takes place at the *crystalline lens* which is suspended directly in the visual path by means of ligaments attached to the *ciliary body*. This structure is formed by a duplication of the choroid coat which, so to speak, is fastened to the sclerotic capsule of the eyeball at about the junction between its anterior one-third and posterior two-thirds. It gives lodgment to a number of smooth muscle cells, many of which are arranged longitudinally to the long axis of the eyeball. In front of the ciliary body, the choroid terminates in the form of the iris, a membranous curtain which applies itself very closely to the anterior surface of the lens, so that only a very narrow space is left here which is filled with aqueous humour.

The lens of the human eye is invested by a capsule which in turn is connected with the ciliary body by means of ligamentous threads. It presents a biconvex shape, its anterior surface always being less convex than its posterior. As such it possesses the power of gathering the rays of light and bringing them to a sharp point of intersection behind it. The spot in which these rays are centralized, is called the *focus*. The general truth here alluded to is familiar to nearly everybody, because if a biconvex lens is held at a certain distance

from a dark wall and a candle is placed in front of it, an image will be formed of the latter upon this screen. The image, however, is upside down, because the rays of light are inverted by the lens.

By moving the candle nearer to and farther away from the lens, it will be found that the image upon the wall enlarges when the distance is decreased. Furthermore, it will be noted that a perfectly clear image is obtained only when the distances between the candle, lens, and screen are adjusted in a particular way. At all other distances the image becomes blurred for the reason that the rays of light are not sharply focalized upon the wall. It is a well known fact that far and near objects cannot be photographed simultaneously. A different adjustment of the lens and sensitive plate of the camera is required for each. One of two methods may be followed in order to obtain a perfectly clear picture: namely, (*a*) the lens may be moved forward for near work or backward for far work, and (*b*) the plate may be drawn backward when receiving the rays of a near object, or forward when a distant object is to be photographed. The fact that the focal distances must be changed in this way everyone can assure himself of by simply placing the candle at different distances from the screen and endeavoring to form a distinct image of it by changing the position of either the lens or the screen.

The Process of Accommodation.—There is still another way in which this adjustment could be effected, namely, to change the refractive power of the lens, and not the position of the lens or screen. Clearly, since the rays of light emitted by a near object must be more quickly converged than those coming from far, near work requires a lens possessing a greater convexity or refractive power. Thus, if a photographic camera could be equipped with a rotary disc carrying a number of biconvex lenses of different power it would fulfill its purpose as well as one in which a single lens is moved forward and backward. The former type of camera, however, is more expensive to manufacture and less convenient to handle; and hence, is of slight value commercially.

Excepting the amphibia, the eyes of all the higher animals

contain a mechanism by means of which their focal power may be altered so as to enable them to form an image of near as well as distant objects upon their retinæ. The manner in which this end is accomplished differs in different animals. Thus, the eyes of the fish are set for near objects, and distant objects are focalized by them by retracting the lens by means of a special muscle attached to its peripheral zone. Certain

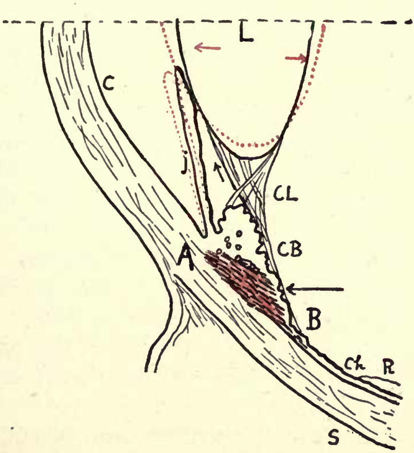


FIG. 143.—Diagram illustrating the process of accommodation in the human eye. *C*, cornea; *L*, lens; *J*, iris; *CL*, ciliary ligament; *CB*, ciliary body; *Ch*, choroid; *R*, retina; *S*, sclera. On near vision the ciliary muscle contracts, drawing the region *B* nearer to region *A*. The tension upon the ciliary ligament being diminished thereby, the lens assumes a more spherical shape, chiefly in the direction of the cornea. This change is indicated in red.

molluscs shorten their eyeballs in the manner of a folding camera, so that the retinæ are actually brought nearer the lens. In brief, it may be stated that all the physical methods of accommodation outlined above find representation in the animal kingdom. The eyes of the mammals are ordinarily set for far objects. Near objects are accommodated for by them by rendering the lens more convex, thereby increasing its refractive power. This method of accommodation corresponds in a way to that physical system which permits us to substitute lenses of varying convexity.

The manner in which the lens of the mammalian eye is adjusted for near vision, has been satisfactorily explained in accordance with the "theory of detention." It is believed that the lens is ordinarily held under a certain degree of tension, which is imposed upon it by the ciliary ligaments and body. At this time it is relatively flat and set for far objects. On near vision the ciliary muscles contract, thereby slightly displacing the ciliary body in a forward direction. This releases the tension upon the ciliary ligaments and substance of the lens, and allows the latter to assume a more convex outline.

The Near Point of the Eye.—When the eyeball possesses a normal shape, and its different parts are thoroughly elastic, the lens is always able to intersect the rays of light upon the retina. But this rule holds true only for those objects which are situated between the horizon and the near point of the eye. It is only natural to suppose that if an object is held very near the eye, the power of the ciliary mechanism must finally fail to impart to the lens a convexity sufficient to converge the rays upon the retinæ. In the normal eye at the age of twenty years, this point lies 10 cm. in front of the cornea. Consequently, any object situated inside the near point cannot be accurately focalized and yields, therefore, a blurred image. As we grow older, the near point moves outward until at about forty years of age it lies 22 cm. from the cornea. General infiltrations and senile changes are responsible for its displacement.

CHAPTER XL

THE STIMULATION OF THE RETINA BY THE RAYS OF LIGHT

The Structure of the Retina.—The retina covers practically the entire concavity of the posterior chamber of the eyeball. It terminates directly behind the base of the ciliary body, forming here a line of demarcation which is termed the ora serrata. Under the high power of the microscope it presents several layers of nervous elements, of which *the rods and cones* are the most important. These cells consist of two segments, which are designated respectively as their outer and inner limbs. The former lie deeply embedded in the pigment cells of the choroid coat, while the latter are directed toward the vitreous humour. Furthermore, while the outer limbs of the rods are cylindrical in shape and exhibit definite cross-striations, those of the cones possess a conical outline and pointed extremity.

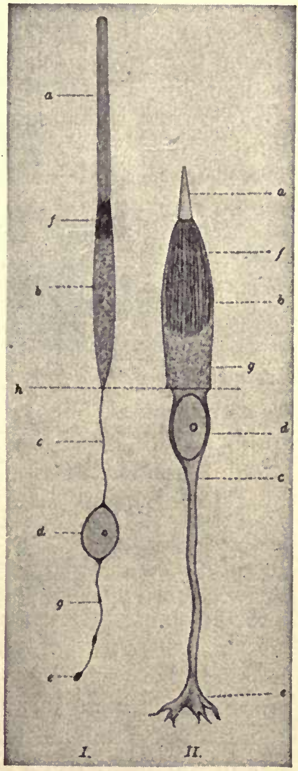


FIG. 144.—I, a rod; II, a cone of mammalian retina; *h*, external limiting membrane. (*G. Greeff.*)

The rods and cones are surmounted by several additional strata of nervous tissue which are designated as the outer nuclear, outer molecular, inner nuclear, and inner molecular.

Each layer embraces a certain number of ganglion cells, possessing different shapes and positions. The fibers arising from these elements pass inward and eventually form a delicate sheet between the vitreous humour and the inner molecular layer, which is marked off against the former by a peculiar network of nervous connective tissue, *the internal limiting membrane.* Naturally, these nerve fibers arise in all parts of the retina and strive toward a common point of exit from the eyeball, which is known as the *optic papilla.* Centrally to this point they form the *optic nerve.*

This perforation in the capsule of the eyeball also serves as the point of entrance for the bloodvessels and lymphatics of the retina, which ramify principally between its internal limiting membrane and inner nuclear layer. It will be seen, therefore, that the nerve fibers are placed in front of the cellular components of the retina and in the direct path of the rays of light. But since this arrangement does not interfere with vision, it must be concluded that a sufficient number of light rays reach the underlying rods and cones in spite of these obstacles. The entrance of the optic nerve or optic papilla contains solely fibers and no rods and cones, nor other cellular elements. Consequently, inasmuch as this particular area cannot be activated by the rays of light, it is appropriately called the *blind-spot.*

The Function of the Retina.—The foregoing discussion must have shown that the retina possesses the power of converting the ethereal vibrations into nerve impulses which finally attain representation in consciousness through the agency of the corresponding center in the cerebrum. Vision is the product of the center and not of the retina. The latter, together with its adjunct structures, merely serves as the mediator between the center and the outside world. The process by which this transfer is effected, is not clearly understood, although it is generally assumed that the retina acts in the manner of a sensitive plate. This theory implies that the rays of light give rise to a reduction of certain pigments which, however, are immediately rebuilt. Upon this basis, the optic impulses would be the results of chemical interactions. This view finds support in the fact that the

retina contains a pigment, called *visual purple,* which may be extracted and dealt with in the manner of any reducible substance. It is true, however, that certain animals are not in possession of this type of pigment, and nevertheless present a perfectly normal acuity of vision. This fact, in conjunction with others to be described later, leads us to infer that the rods and cones themselves are sensitive to light, and employ the visual purple merely as an activating substance to intensify the rays of low striking force.

The Blind Spot.—A simple experiment which may be performed to prove that the optic papilla is insensitive to the rays of light, is the following: Close your left eye and with your right eye look steadily at the cross of Fig. 145, held at a distance of about 20 cm. from its cornea. Now, move the

FIG. 145.—Diagram to demonstrate presence of blind spot in the visual field. Fix the cross with the right eye; bring figure closer to eye until the white dot appears. (*Helmholtz.*)

figure towards you until the black dot disappears. At this distance the rays emitted by the dot fall upon the papilla of this eye and are not perceived. Naturally, the moving of the figure still closer to the cornea will cause the dot to reappear, because the rays previously focalized upon the blind spot, must then leave this area and again strike the retina proper.

When both eyes are used in vision, this fact that the optic papillæ are insensitive to light, cannot give rise to visual disturbances, because while the rays emitted by an object may fall upon the blind spot of one eye, they must then strike the outlying districts of the opposite retina. The latter sensation overcomes the defect in the opposite visual field. In this connection, brief reference should also be made to the fact that the rays entering the eyes under normal conditions, are not focalized upon anatomically related areas. But,

although the visual elements involved occupy different positions in the two retinæ, the sensations mediated by them are perfectly harmonious in their character.

The Yellow Spot.—About 3.5 mm. to the outside of the blind spot lies the yellow spot or macula lutea, which forms the most sensitive area of the retina. Structurally, this region is differentiated from the remaining portion of the retina by the fact that it contains solely a large number of closely-set cones. It is also noted that these elements are here directly exposed to the entering rays of light, while elsewhere they are covered by several layers of cell-bodies and fibers. Furthermore, inasmuch as the visual purple is an adjunct of the rods, it is found in all parts of the retina but not in the yellow spot. The diameter of this area measures 2.0 mm., whereas that of the blind spot measures 1.8 mm.

Functionally, the macula lutea is differentiated from the remaining regions of the retina by the fact that it is much more sensitive to light than the others. Thus, clear vision invariably requires us to bring the object in a direct line with the center of the macula, designated as the fovea centralis. This end is accomplished by the contraction of the external muscles of the eyeball. In dim light, on the other hand, we always endeavor to focalize the object upon the outlying districts of the retina, activating thereby the rods and visual purple. Thus, *direct vision* is mediated by the cones and is employed in high intensities of light, while the rods are the elements of *indirect vision* and are activated with the aid of the retinal pigment by rays of low striking force.

It is a matter of common experience that visual impressions are obtained not only during the periods of retinal stimulation but persist for some time thereafter. Furthermore, the duration of the initial excitation is often surprisingly brief, because a flash of lightning lasting only $\frac{1}{1,000,000}$ sec., is sufficient to evoke a sensation. The successive stimulations, however, must be separated from one another by appreciable intervals, otherwise a fused impression will be obtained. Thus, a luminous rod if turned around at a steadily increasing speed, finally yields a continuous circular visual concept.

This principle is employed in cinematography to reproduce the movements of objects. A series of instantaneous photographs taken of an object in motion, are projected in quick succession upon a screen, so that the succeeding one always produces its impression before that of the preceding one has died out. In order to accomplish this fusion not less than ten photographs must be consecutively projected in the time of one second.

Optical Defects of the Eye.—The purpose of the normal eye is to bring rays of light to a precise intersecting point upon the retina. An eye that is able to accomplish this end, is said to be emmetropic. Accordingly, the condition of *emmetropia* signifies normal vision. Contrariwise, an eye which is unable to focalize the rays of light precisely upon the retina, is characterized as ametropic. This condition of abnormal refraction, which is known as *ametropia*, may be due to the following causes:

(*a*) imperfect curvature of the cornea, astigmatism,
(*b*) diminished elasticity of the lens, presbyopia,
(*c*)imperfect shape of the eyeballs:

1. Myopia, the eyeball is too long,
2. Hypermetropia, the eyeball is too short.

Probably the most prevalent condition is *presbyopia*, which is due to a loss of the elasticity of the lens. Usually about the forty-fifth year of our life, certain changes begin to make themselves felt which are characterized by general infiltrations of our tissues, rendering them less pliable. The crystalline lens does not form an exception to this rule, and hence, it is noted that it becomes increasingly inflexible. For this reason, it can no longer be rendered so convex as formerly. A flat lens is employed to focalize distant objects. Consequently, the presbyopic eye is unable to form a perfectly clear image of near objects. This difficulty is remedied by placing a biconvex lens in front of the eye whenever near vision is required.

It is true that practically every eye is slightly astigmatic, because the different prismatic elements of its lens are not arranged as in a perfect optical system. This "normal"

degree of *astigmatism* does not give rise to actual disturbances in vision. The usual cause of the development of astigmatic aberrations is an unequal curvature of the cornea, causing a distortion of the bundle of light as it traverses this membrane. Obviously, that segment of the cornea which possesses the greatest convexity, must bring the entering rays of light more quickly to a focus than the less convex. As a rule, these differences in the curvature of the cornea, are placed at right angles to one another, and affect chiefly its horizontal and vertical meridians.

The conditions of *near-sightedness* or *myopia* and *far-sightedness* or *hypermetropia*, are due to a faulty shape of the eyeball,

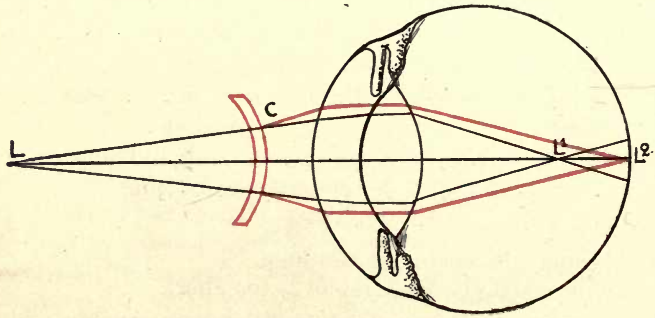


FIG. 146.—Diagram to illustrate the refraction in a myopic eye. *L*, luminous point focalized in L^1 in the vitreous humor. A concave lens *L* renders these rays more divergent so that they are made to intersect upon the retina in L^2.

arising in consequence of inherited abnormalities and acquired errors in reading. Thus, the eyeball may lengthen in the course of time until the focal point of the light rays comes to lie in the vitreous humor. Behind this point, the rays again diverge and finally strike the retina far apart. In this way, a dispersion circle of light is formed upon this receptor which cannot yield a perfectly clear image. Furthermore, this image cannot be rendered more precise by extra efforts at accommodation, because all greater degrees of convexity of the lens must force the focal point farther forward into the vitreous humor, thereby increasing the size of the circle of dispersion upon the retina.

A person whose eyeballs are too long, cannot form a clear image of distant objects, although he is well able to focalize near objects. For this reason, this condition is known as *near-sightedness* or *myopia*. In order to remedy it, the focal point must be moved farther backward until it strikes the retina. This end is accomplished by placing a biconcave lens in front of the cornea which presents the eye with rays of light more divergent than they would be otherwise.

The condition of *far-sightedness* or *hypermetropia* arises when the eyeball is shorter than normal, so that the focal

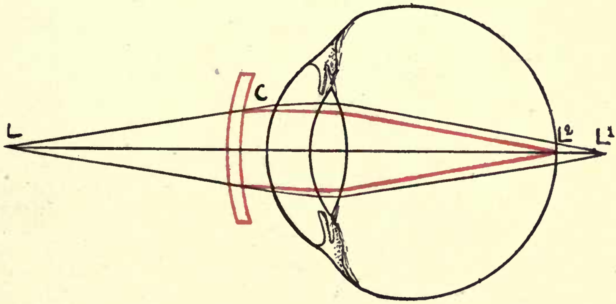


FIG. 147.—Diagram to illustrate the refraction in a hypermetropic eye. L, luminous point focalized in L^1 "behind" the retina. A convex lens C renders these rays more convergent so they are made to intersect upon the retina in L^2.

point falls behind the retina. Consequently, the rays of light must strike the retina while still far apart, and cannot, therefore, give rise to a precise image. A person whose eyeballs are too short, cannot see objects near him very distinctly, although he can accommodate for them in a measure by rendering the lens especially convex by making extra efforts at accommodation. This condition may be remedied by placing a biconvex lens in front of the cornea which renders the entering rays of light more convergent than they would be otherwise. This enables the eye by its own efforts to bring the focal point farther forward until it comes to lie precisely upon the retina.

INDEX